THE UNIVERSITY OF ALBERTA

OSTEOLOGY OF KINDLEIA FRAGOSA JORDAN (HOLOSTEI: AMIIDAE), FROM THE EDMONTON FORMATION (MAESTRICHTIAN) OF ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Osteology of Kindleia fragosa Jordan (Holostei: Amiidae), from the Edmonton Formation (Maestrichtian) of Alberta", submitted by Donald Edward O'Brien, B.Sc., in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

Articulated specimens of Kindleia fragosa Jordan (Holostei: Amiidae) from a single locality in the upper part of the Maestrichtian Edmonton Formation permitted a reconstruction of its skeleton. Grossly, the skeleton of Kindleia closely resembles that of Amia calva Linné, but the following features are seemingly more primitive: the skull is shorter and more robust, the orbit is larger, the postorbitals cover more of the cheek, and the tail is more distinctly abbreviated heterocercal. The numerous, flat-crowned, pharyngeal teeth of Kindleia are specialized for a somewhat more durophagous diet than that of Amia. Kindleia probably represents an offshoot from the more generalized, predaceous line of evolution that led to Amia.

ACKNOWLEDGEMENTS

I am grateful to Dr. R.C. Fox, who supervised this study; his interest, assistance and suggestions were invaluable. I thank Mr. L.A. Lindoe for his aid in the preparation and illustration of specimens, and I thank my wife, Connie, for her help and encouragement and the typing of preliminary drafts of this thesis. Mr. F. Dimitrov assisted in the preparation of the plates and Mrs. D. Haugan typed the final copy.

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INTRODUCTION

In the summer of 1967, field parties from The University of Kansas, Lawrence, Kansas, and The University of Alberta, Edmonton, Alberta, discovered and collected samples of a "fish-bed" from the Edmonton Formation. The material described in this manuscript produced the first articulated skeletal study of Kindleia fragosa Jordan.

The fossils occur in a thin bed within a large, slumped block on the north wall of an east-west coulee in the valley of the Red Deer River. The locality (Fig. 1) is about twelve miles northeast of Trochu, Alberta, approximately central in Lsd. 3, Sec. 32, Tp. 34, R. 21 W., west of the 4th meridian.

Numerous workers have studied and described the stratigraphy of the Edmonton Formation (Selwyn, 1874; Tyrrell, 1887; Allan and Sanderson, 1945; Sternberg, 1947; Elliot, 1960; and Ower, 1960). Allan and Sanderson (1945) formalized the name "Edmonton Formation" for rocks between the Bearpaw Shale and the erosional unconformity at the base of the Paskapoo Formation, and in the same report, Sanderson divided the formation into three members: "the Upper, Middle and Lower Edmonton members". These three members were initially adopted by Srivastava (1965), but he later (1968) devised the terms "upper, middle and lower Edmonton Divisions". Ower (1960) separated the Edmonton Formation into five members (A to E), but Lillegraven (1969) used the expression "the upper part of the Edmonton Formation", or "the upper Edmonton Formation", since no tripartite division of the entire formation "that agreed with accepted nomenclatorial procedure" had yet been formalized. I shall follow Lillegraven's terminology.

A study of the paleontology of the Edmonton Formation began in the mid 1880's when J.B. Tyrrell discovered dinosaur bones along the Red Deer River (Russell and Chamney, 1967). L.M. Lambe, B. Brown, C.H. Sternberg, G.F.

Sternberg, D.A. Russell and notably C.M. Sternberg (see Russell and Chamney, 1967, and Langston, 1965, for historical reviews and bibliographies) were important among those who continued the study of vertebrate fossils of the Edmonton Formation. Bell (1949) reported on the megaflora; Srivastava (1965, 1966, 1967, and 1968) described the microflora, and Tozer (1956) studied the freshwater molluscs of the formation. Lillegraven (1969) examined the mammalian fossils of the upper part of the Edmonton Formation, but no one has yet extensively studied the smaller, non-mammalian vertebrates from any part of the formation.

Jordan (1927) named and described Kindleia fragosa from several fragments (including a type dentary and referred plates with peg-like teeth) from the upper part of the Edmonton Formation and assigned the genus to the Family Cichlidae, Infraclass Teleostei. Russell (1928a) described an amiid, Stylomyleodon lacus, from the Paskapoo Formation (Paleocene) of Alberta. The type specimen is a fragment of a vomer (= "left splenial", UA 131, Department of Geology; The University of Alberta) that bears numerous stout, peg-like teeth; referred specimens include dentaries, dermal plates, vertebrae, scales and fragments of the skull (UA 133, Department of Geology, The University of Alberta). In 1928, Jordan drew attention to the priority of Kindleia fragosa over Stylomyleodon lacus, but Russell (1928b; 1929) maintained that the dentaries of the two genera were different. Estes (1964) recognized synonymy of Kindleia and Stylomyleodon, and from the study of disarticulated bones he diagnosed Kindleia fragosa as "an amiid with frontals about three times the length of the parietals; large lower postorbitals, the lower one expanded; frontals with excavations for orbits; palatal teeth stout, styliform crushers; operculum subrectangular; branchiostegal rays distally rounded".

Amia calva, the only modern amiid, lives chiefly in quiet water swamps

and lakes (although it is also found in sluggish rivers) in the Mississippi and St. Lawrence drainage systems (except Lake Superior) (Hubbs and Lagler, 1947:40). The genus has a large head, shielded by thin, bony plates, a large mouth, a long, low dorsal fin, an abbreviated, heterocercal tail and large, cycloid scales (Jordan and Evermann, 1896:112). Individual fish may reach a length over 2 feet and a weight over 10 pounds, although the average weight is 2 to 3 pounds; individuals are extremely voracious, feeding mainly at night on various kinds of animal life, but predominantly on fish and crayfish (Hubbs and Lagler, 1947:40).

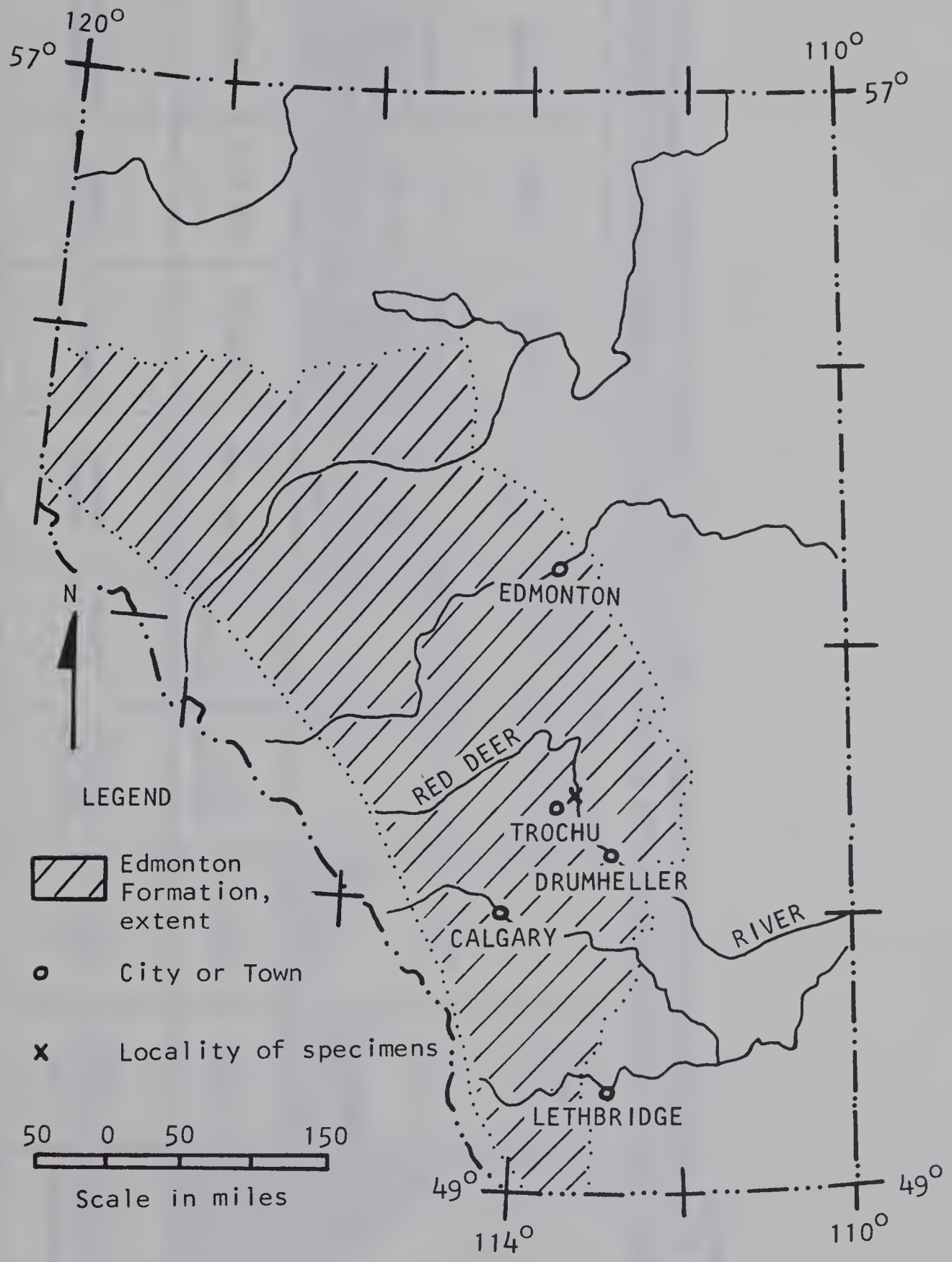


Fig. 1. An outline map of Alberta.

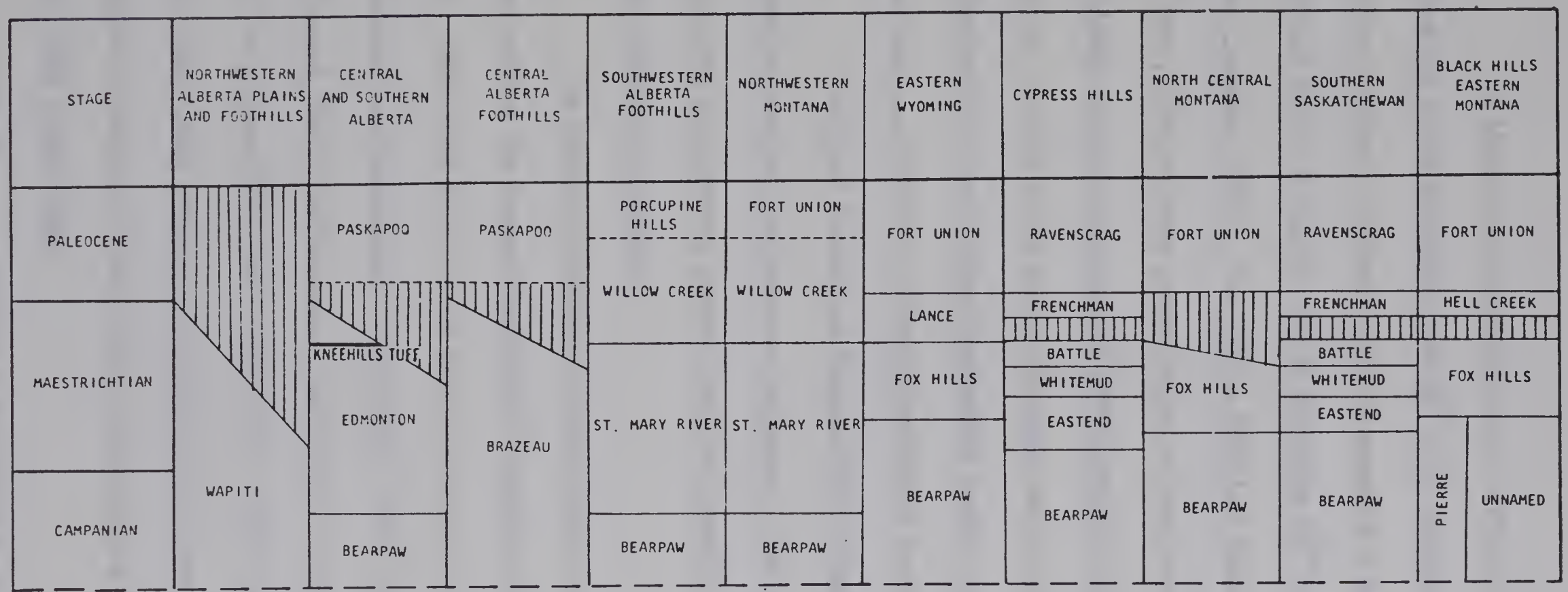


Fig. 2. Correlation chart of uppermost Cretaceous and Paleocene Formations fo the western plains and foothills of Canada and the U.S. (modified after Williams and Burk, 1964:169, Taylor, Mathews and Kupsch, 1964:192 and Tozer, 1956, fig. 2).

GEOLOGIC SETTING

The Upper Cretaceous Edmonton Formation (Fig. 1) extends in Alberta at the surface and in the subsurface from 55° north latitude south to the United States border, and from the Rocky Mountain foothills eastward to longitude 114° in the north, to longitude 113° in the south, and to longitude 112° in the center (Williams and Burk, 1964; Campbell, 1967). The 1300 to 2600 feet (Russell and Chamney, 1967; Williams and Burk, 1964) of strata consist mainly of poorly-sorted sandstones and siltstones high in feldspar content and cemented with bentonitic clay (Allan and Sanderson, 1945); however, the 200 to 290 feet of the upper part of the formation are composed predominantly of well-sorted, moderately coarse, quartzose sandstone low in clay constituents and with minor interspersed beds of ironstone and coal (Sternberg, 1947).

The Upper Cretaceous Bearpaw Shale underlies, and the Paleocene Paskapoo Formation overlies, the Edmonton Formation. The top of a grey, very fine-grained, marker bed about twelve inches thick, the Kneehills Tuff, delimits the base of the upper Edmonton Formation.

The Edmonton Formation (Maestrichtian) is correlated (Fig. 2) with the upper parts of the Brazeau and Wapiti Formations of the Rocky Mountain foothills (Bell, 1949); with the St. Mary River and lower part of the Willow Creek Formations of southern and southwestern Alberta (Bell, 1949; Tozer, 1956); the Eastend, Whitemud, Battle and Frenchman Formations of central and southeastern Alberta and the Cypress Hills (Bell, 1949; Richie, 1960; Campbell, 1962); and the Fox Hills, Hell Creek and Lance Formations and chronologically with part of the Bearpaw Formation of North Dakota, Montana and Wyoming (Fraser et al., 1935; Bell, 1949; Tozer, 1956).

Potassium-argon dating of the biotite and sanidine in the bentonites of

the upper part of the Bearpaw Formation and in the Kneehills Tuff produced ages of 68 million years and 65 to 66 million years, respectively (Baadsgaard et al., 1964); the Cretaceous-Tertiary boundary has an age of approximately 64 million years (Folinsbee et al., 1965). Therefore, the Edmonton Formation and the upper part of the Edmonton Formation represent approximate intervals of deposition of four million and one to two million years, respectively.

Deposition of the Edmonton strata was mainly continental in freshwater basins, mud flats, flood plains and deltas along the fringes of an easterly retreating Bearpaw sea (Allan and Sanderson, 1945). The climate and geography changed from humid, subtropical, lacustrine at the time of deposition of the lower Edmonton Formation, to cooler, warm - temperate, fluvial with savanna-type vegetation at the time of deposition of the lower part of the upper Edmonton Formation, to forested, warm - temperate at the time of deposition of the uppermost part of the formation (Srivastava, 1968). The occurrence in the Edmonton beds of fossils of aquatic plants and coniferous trees suggests the original presence of both marshy and forested areas (Bell, 1949; Srivastava, 1968).

PALEONTOLOGY

Preservation

Except for the well-ossified, external bones of the skull, the skeleton of Kindleia, especially the braincase, suspensorium and fin rays, tends to be poorly preserved and often partly disarticulated. The bone is soft and easily fragmented, and the host rock is poorly cemented.

The fine detail of preservation and the presence of articulated skeletal parts suggest that transportation of the bone after death was not extensive. However, burial probably was not immediate since incomplete fragments are represented; it is likely that the place of death was not far from the site of deposition.

The deep brown color of the bone implies post-mortem deposition of iron, a feature expected in the bone preserved in the ironstone-rich sandstones of the upper part of the Edmonton Formation.

Measurements and Illustrations

The maximum length (the dimension parallel to the midline), width (the dimension perpendicular to the length), and other measurements, where warranted, of the undamaged bones of Kindleia fragosa and their homologies in Amia calva were measured with dividers. The results are presented in Table I of the Appendix; a summary of these data for Kindleia showing the range and average measurement - e.g., range 6-9 (average 7.5) mm. - is given under a subheading, "Measurements", in the anatomical description of each bone.

Line drawings for each bone that is discussed in the anatomical description occur in the text; these consist of composite drawings of each ossification of Kindleia

and illustrations (using largely a single disarticulated skull) of the corresponding bone of Amia. Photographs of articulated fossil specimens and complete isolated bones are included in the plates at the back of the manuscript.

Terminology

The skeletal anatomy is described under numerous subheadings, most of which are fairly explicit; a few, however, require explanation: the dermal roof of the skull includes a shield of bone over the top and sides of the head and bones of the upper jaw; the palatal complex includes dermal bones in the roof of the mouth (except the parasphenoid) and ossifications of the palatoquadrate; the braincase consists of internal endochondral bone, cartilage, and the dermal parasphenoid; the opercular series (the operculum, subopercular and interopercular) forms a flap of bone over the gill region between the head and the pectoral girdle, and the branchiostegal rays and the gular cover the area between the rami of the lower jaw; the hyoid arch (which includes the hyomandibular) forms the main support for the gills (Romer, 1962).

The terms anterior, posterior, lateral, medial, ventral and dorsal or combinations of these are used in describing the orientation of bones. The terms external and internal (palatal in some instances) refer to the surfaces of the bone that either face or face away from the longitudinal axis of the body. The phrase lateral line canal is used for the skull and trunk, but other workers (including G.E. Jarvik, B.G. Gardiner, E.A. Stensio, C. Dechaseaux and R. Estes) designate the lateral line system within the skull as the sensory canal system. The descriptive terminology follows mainly that of Norden (1961) and Estes (1964). The synonymies include most alternative terms applied to the bones of Amia or closely related forms.

The following abbreviations are used: C.N., cranial nerve, UA, collection of The University of Alberta.

Description of Materials

Class OSTEICHTHYES
Infraclass HOLOSTEI
Order AMIIFORMES
Family AMIIDAE

Kindleia fragosa Jordan

Kindleia fragosa Jordan, 1927, p. 146, figs. 1 - 14.

Stylomyleodon lacus Russell, 1928a, p. 104, figs. 1 - 4.

Kindleia fragosa Estes, 1964, p. 29, figs. 15b, 16e, 18b.

Ossifications of the Dermal Roof of the Skull

EXTRASCAPULAR (scalebone, Gregory, 1933; tabular, Berg, 1940; postparietal, Goodrich, 1930)

Specimens examined.-- UA 5398, complete left and right; UA 5416, complete left; UA 5449, complete left; UA 5482, complete left; UA 5486, complete right; UA 5498, incomplete right; UA 5503, nearly complete left.

Measurements.-- Length, 6-9 (8) mm.; minimum length, 2-3.5 (3) mm.; width, 17-23 (20) mm.

Illustrations.-- Fig. 3; Plate I, Fig. 1, Fig. 2.

Description.-- The wing-shaped extrascapular extends in its greatest dimension from the roof edge, where it is rounded and longest, to the midline, where it is squared and shortest. In its lateral half the length decreases little, but in its medial half the extrascapular tapers abruptly. The anterior edge of the bone abuts against and slightly overlaps the posteroventral shelves of the pterotic and the parietal; the posterior edge overlaps the anterodorsal surface of the suprascapular.

On the external surface of the extrascapular, small pits (of the lateral line system) extend linearly along the lateral and posterior edges; grooves and ridges radiate from a focus slightly anterior and lateral to the center. On the internal surface a transverse ridge for the lateral line canal extends from near the anterolateral corner (where it is most pronounced) to the midline; on either side of this ridge near the roof edge are two large foramina for the passage of the longitudinal lateral line canal from the pterotic to the suprascapular; more centrally are numerous small openings for the supratemporal branch of C.N. X (Allis, 1897, fig. 19).

Discussion. -- The extrascapular of Kindleia fragosa is shortest medially and longest at the roof edge (as in Amia calva), but the decrease in length medially is more abrupt in Kindleia, especially in the medial half of the bone. In Amia, the taper is more uniform along the width of the bone, and the outline of the extrascapular is more asymmetrical than in Kindleia owing to a prominent posterolateral projection. The lateral line pits, the openings for the supratemporal branch of C.N. X and the ornamentation are nearly the same in size, pattern and position in Amia and Kindleia. The internal surfaces in both genera have the central, transverse ridge, but in Kindleia, the longitudinal canal between the large foramina is oriented almost perpendicularly to the internal ridge; in Amia, the longitudinal canal is more oblique to the transverse ridge with the anterior foramen relatively more medial. A distinct indentation present in Amia immediately adjacent and medial to the anterior foramen is not seen in Kindleia; the significance of its absence in Kindleia is unknown, but in Amia, a cartilaginous extension of the posterior margin of the pterotic fits into the indentation, possibly as a new point of articulation.

Estes (1964:30) stated: "There are no differences from the same bone in Amia calva," and yet his reconstruction of the skull of Kindleia (fig. 18b:38) shows differences from Amia comparable to those noted above.

PTEROTIC (squamosal, Allis, 1897; pterotic-intertemporal, de Beer, 1937; supratemporal, Romer, 1962; dermopterotic, Janot, 1967)

Specimens examined.-- UA 5398, complete left and right; UA 5416, complete left; UA 5421, complete left; UA 5426, complete right; UA 5450, complete right; UA 5456, complete left; UA 5460, incomplete left; UA 5492, complete left.

Measurements.-- Length, 16-25 (20) mm.; width, 6-10 (8) mm.; minimum width, 2-3 (2) mm.

Illustrations.-- Fig. 4; Plate I, Fig. 1, Fig. 2; Plate II, Fig. 1, Fig. 2.

Description.-- The pterotic is a nearly wedge-shaped, posterolateral, roofing bone with a prominent, anterior lappet that suturally meets the posterior edge of the dermosphenotic and that intervenes between the dorsal postorbital and the frontal. Along the posterior margin of the pterotic is a short, smooth shelf that fits under the anterior edge of the extrascapular; the lateral edge of the shelf flares slightly posterolaterally. Another wider shelf along the anterior and middle part of the medial edge of the pterotic underlies the lateral parts of the frontal and parietal; the shelf has two excavations (one anterior for the frontal and another more posterior for the parietal). A rather wide, ventrally directed flange that runs anteroposteriorly along the internal surface and that curves laterally in the posterior quarter of the bone extends down to meet (and is attached by cartilage to) the opisthotic. On the external surface of the pterotic, ridges and grooves radiate outward from a point near the center. A row of lateral line pits that

connects in front with the lateral line canal of the dermosphenotic and behind with the canal of the extrascapular roughly parallels the lateral margin of the pterotic; near the posterior edge of the bone, a lateral branch of the longitudinal canal joins with the lateral line canal of the preoperculum. A line of pits (lacking a visible canal) crosses the pterotic and the parietal near their posterior edges. Internally, the surface of the pterotic is relatively smooth.

Discussion.-- The pterotics of Kindleia and Amia resemble each other in size, shape and ornamentation but for the prominent notches in the pterotic of Kindleia for the lateral flanges of the frontal and parietal (as Estes noted, 1964:30; fig. 18b:38); these notches decrease the width of the ornamented external surface of the pterotic and increase the width of the medial shelf. The anterior lappet (likely formed by the constriction in width of this part of the bone by the anterior notch for the frontal) is usually more prominent in Kindleia than in Amia, contrary to what Estes illustrated (1964, fig. 18a:38) for the right parietal of Amia. In the seven skulls of Amia that I examined, only one (the smallest individual) had a prominent anterior lappet of the pterotic comparable to that seen in Kindleia. The lateral line system of the pterotics of Kindleia and Amia are much alike, and are not as different as figured by Estes (1964, fig. 18:38). The confusion exists because Amia often bears an additional system of pits (shown vaguely by Allis, 1897, fig. 1) that varies considerably in surface depth and extent. This system (when complete) extends posterolaterally from the center of the frontal and bifurcates in the posterior part of the bone; one branch enters the pterotic at its anteromedial corner and then connects with the longitudinal canal of that bone, and the other branch extends posteromedially into the parietal. Estes (1964, fig. 18a) and Janot (1967, fig. 1:141) have mistaken part of this additional system as the main canal of the pterotic and

have overlooked the extension of the longitudinal canal of the pterotic into the dermosphenotic that is actually present in Amia, as in Kindleia. The additional line of pits seen in Amia is not clear in the sample of Kindleia from the Edmonton Formation, although Estes (1964, fig. 18b) showed a part within the frontal.

PARIETAL

Specimens examined. -- UA 5398, complete left and right; UA 5416, complete left; UA 5421, complete left; UA 5426, complete right; UA 5450, complete left and right; UA 5456, complete left and right; UA 5471, incomplete right; UA 5492, incomplete right.

Measurements. -- Length, 10-13 (12) mm.; width, 9-15 (12) mm.

Illustrations. -- Fig. 5; Plate I, Fig. 1, Fig. 2; Plate II, Fig. 1, Fig. 2.

Description. -- The almost square parietal, a well-ossified, posteromedial roofing bone, has a long anterior flange that suturally underlies the posterior part of the frontal, producing a nearly straight suture. A short posterior shelf of the parietal extends under the anterior edge of the extrascapular. Laterally, most of the edge of the parietal forms a flange that intrudes into a notch of the pterotic, except in the posterior quarter where an unornamented ventral shelf fits under the posteromedial edge of the pterotic. Medially, where the inter-parietal suture is broadly S-shaped, the edge of the posterior part of the left parietal is notched and has a wide ventral shelf that underlies a flange of the right parietal; more anteriorly, the left parietal overlaps onto a narrow ventral shelf of the right parietal. The external surface of the parietal bears grooves and ridges that usually spread outward from a point about one-quarter the distance from the middle of the posterior edge; also, about one-third the distance from the posterior edge, a shallow groove bearing

lateral line pits crosses from the pterotic to the midline, and another shallower line of pits extends anteroexternally within the parietal from a point near the center of the transverse groove. The internal surface of the parietal is smooth.

Discussion. -- The size, shape and ornamentation of the parietal of Kindleia resemble that of the parietal of Amia, but the course of the frontal-parietal suture is less variable in Kindleia. Estes (1964:30) recognized the presence of a "broad squamous suture" of the parietal under the frontal "exposing much less of its length than in the Recent species". The undulating pattern of the suture in Amia produces a considerable range in the length of the ornamented part of the parietal, but generally the length is less in Kindleia than in Amia, although the total lengths of the bones in the two genera (including flanges and ventral shelves) are much the same. In Amia, the inter-parietal suture varies from almost straight to S-shaped as in Kindleia, but the excavation in the left for the right and the ventral shelf of the left that underlies the right are usually wider in Kindleia and not narrower as Estes illustrated (1964, fig. 18:38). Estes (1964:30) noted that in one-third of his fossils the excavation was in the right and two-thirds in the left; in all the specimens from the Edmonton Formation, the left is notched. The transverse line of pits is much alike in the two genera, and in Kindleia, the anteroexternal line is short as in some skulls of Amia (Estes, 1964, fig. 18a). In other Recent individuals, the anteroexternal canal continues anteriorly into the frontal and joins there with a branch from the pterotic (see the discussions of the pterotic and parietal, or Janot, 1967:fig. 1).

FRONTAL

Specimens examined. -- UA 5398, posterior part of left and right; UA 5402, incomplete right; UA 5421, nearly complete right; UA 5426, incomplete

right; UA 5434, incomplete right; UA 5450, nearly complete right; UA 5456, complete left and right; UA 5462, incomplete left; UA 5477, part of right over orbit; UA 5481, anterior part of right; UA 5484, incomplete right; UA 5493, central part of right; UA 5507, complete right.

Measurements.-- Length, 26-36 (30) mm.; width, 11-19 (15) mm.; minimum width, 6-9 (8) mm.; depth of excavation for the orbit, 2-3.5 (3) mm.

Illustrations.-- Fig. 6; Plate I, Fig. 1; Plate II, Fig. 1, Fig. 2; Plate IV, Fig. 1, Fig. 2.

Description.-- The frontal is a long, nearly rectangular, dermal, roofing bone with a lateral edge that is gently tapered medially from posterior to anterior, to a point midway along its length; anterior to this, the bone is deeply excavated for the orbit to a depth about half of its maximum width. The frontal suturally overlaps the parietal posteriorly, the pterotic posterolaterally, the dermosphenotic laterally and the premaxilla anteroventrally; directly in front, it is separated from the nasal and adnasal by an unossified gap, the parethmoid, which in life was probably filled with cartilage. The paired frontals meet at the midline along a slightly wavy suture formed by overlap of one of the pair (usually the left) on a narrow medial shelf of the other. Externally, a system of ridges and grooves radiate from the center; a series of lateral line pits extends anteromedially from the dermosphenotic to the center of the bone and then to the anterolateral corner. On the internal surface (visible only in two specimens, UA 5477, UA 5462), a prominent ridge housing the supraorbital canal of the lateral line system runs anteroposteriorly near the rim over the orbit; a second, fainter ridge arises near the center of the frontal with the first and extends anteromedially forming a narrow, slightly depressed V with the main ridge. A groove at the edge of the orbital

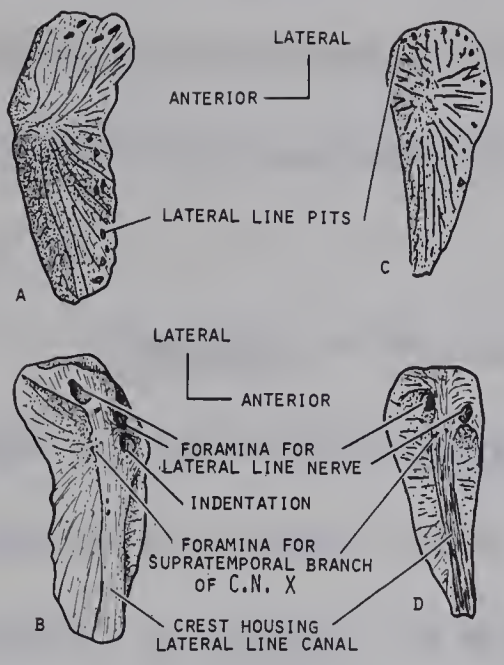


FIG. 3. EXTRASCAPULARS: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

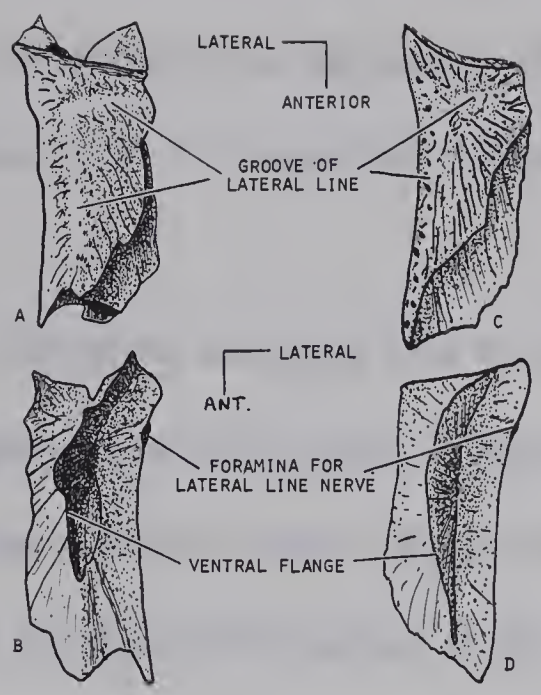


FIG. 4. PTEROTICS: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

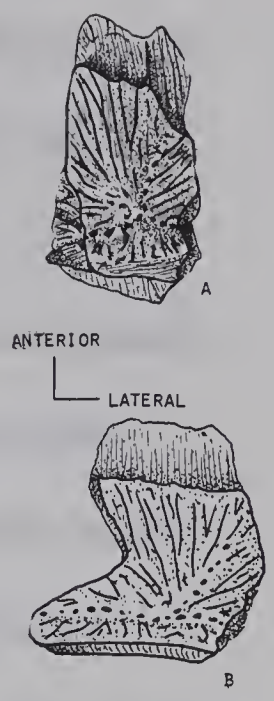


FIG. 5. PARIETALS: A, AMIA, B, KINDLEIA, EXTERNAL SIDE OF RIGHT.

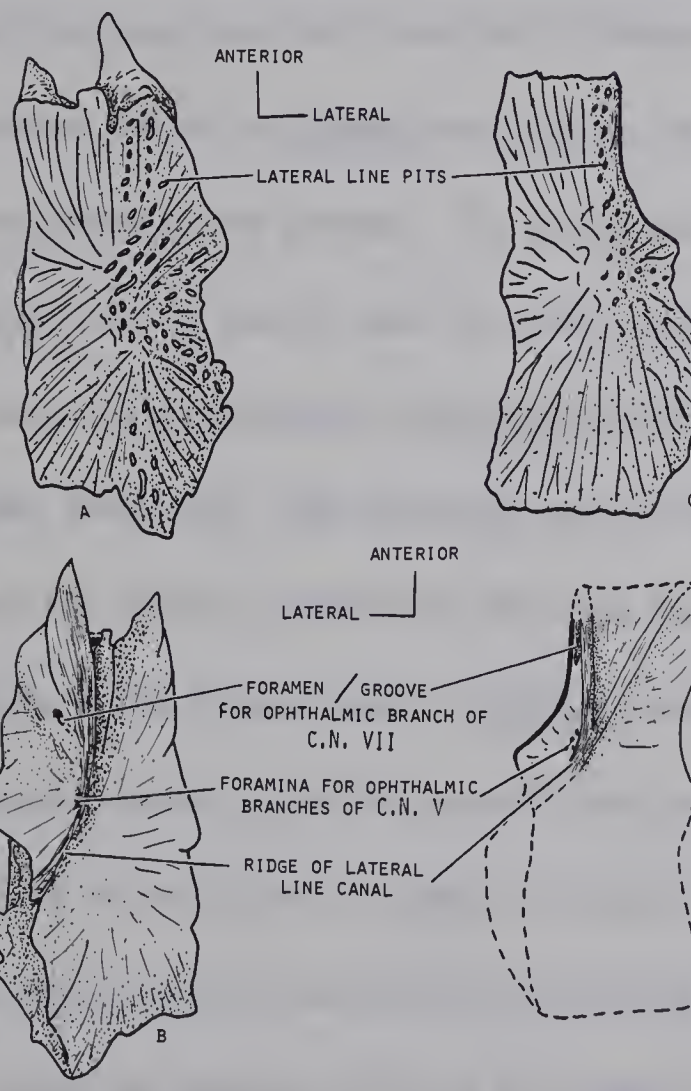


FIG. 6. FRONTALS: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

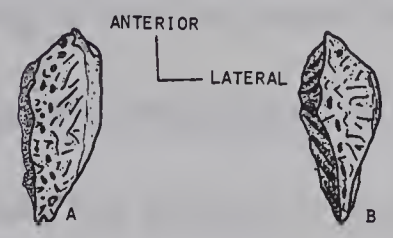


FIG. 7. DERMOSPHENOTICS: A. AMIA, B. KINDLEIA. EXTERNAL SIDE OF RIGHT.

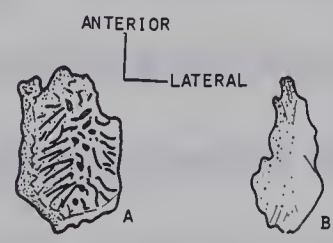


FIG. 8. NASAL: A, EXTERNAL SIDE OF RIGHT OF AMIA. ADNASAL: B, EXTERNAL SIDE OF RIGHT OF AMIA.

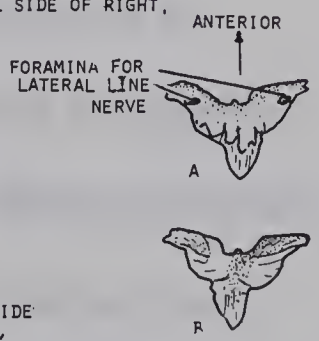


FIG. 9. ROSTRAL: AMIA; A, EXTERNAL SIDE; B, INTERNAL SIDE.

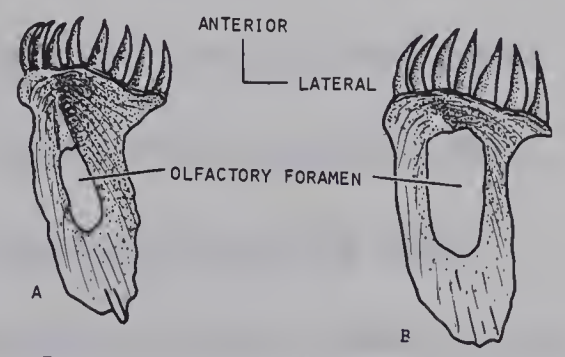


FIG. 10. PREMAXILLAE: A, AMIA, B, KINDLEIA, EXTERNAL SIDE OF RIGHT.

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

excavation on the lateral side of the more prominent ridge and numerous small foramina near the center of the bone are probably for the passage of divisions of the ophthalmic branch of C.N. VII and C.N. V, respectively (Allis, 1897, fig. 19).

Discussion. -- The frontals of Kindleia and Amia have the same general shape, but the frontal of Kindleia appears relatively longer, is more broadly excavated for the orbit, and is narrower anteriorly than in Amia (as Estes noted, 1964:30). In Kindleia, the length of the ornamented surface of the frontal is three times the length of the same surface of the parietal, while in Amia, it is only two and one-half times; this difference is owing to the less wavy frontal-parietal suture in Kindleia and also to the greater part of the parietal of Kindleia that underlies the frontal. The medial suture between the frontals is wavy in each genus, but the medial shelf is wider in Kindleia. The ornamentation and the external pits are similar in Kindleia and Amia (and like that figured for Kindleia, Estes, 1964, fig. 18b, although none of the specimens from the Edmonton Formation have the central, posteriorly directed line of pits), but the pits anteriorly are nearer to the lateral edge in Kindleia owing to the depth of the orbital rim. As discussed above under the pterotic and parietal, a second set of pits is sometimes present on the frontal of Amia; it extends from the center of the external surface posteriorly and bifurcates with one branch entering the pterotic and the other entering the parietal. This is the lateral line system shown by Estes (1964, fig. 18a) for the frontal of Amia, but the main line that extends (as in Kindleia) laterally into the dermosphenotic and the longitudinal line from the dermosphenotic to the pterotic are not depicted. The internal surface of the frontal of Kindleia is much like that of Amia with differences attributable to the depth of excavation for the

orbit. The anterior part of the internal ridge is tangential to the rim of the orbit in Kindleia, but is apart from the rim in Amia. In Kindleia, a groove over the orbit hugs the lateral side of the ridge, but in Amia, a foramen (instead of a groove) opens midway between the outer edge of the bone and the ridge; the groove or foramen is likely for the passage of an ophthalmic branch of C.N. VII (Allis, 1897, fig. 19). In Amia, the depressed area between the two ridges, which is deeper than in Kindleia, and to which I assume Estes (1964:30) referred to as "rugose depression", carries the superficial ophthalmic branch of C.N. VII (Allis, 1897, fig. 19). The numerous central foramina in Amia (and also probably in Kindleia) are for the passage of the subcutaneous ophthalmic branches of C.N. V(ibid).

DERMOSPHENOTIC (postfrontal, Allis, 1897, Goodrich, 1930)

Specimens examined. -- UA 5398, complete left; UA 5402, incomplete right; UA 5426, incomplete right; UA 5450, complete right; UA 5460, complete left; UA 5493, complete right.

Measurements. -- Length, 10-12 (10.5) mm.; width, 4-5 (4) mm.

Illustrations. -- Fig. 7; Plate I, Fig. 1; Plate II, Fig. 1; Plate IV, Fig. 1.

Description. -- The small, tear-shaped dermosphenotic is a marginal roofing ossification, narrowest posteriorly at the anterior lappet of the pterotic. Anteriorly, the dermosphenotic forms a part of the posterior border of the orbit; laterally, it curves slightly downward to form a narrow platform for articulation with the anterodorsal part of the dorsal postorbital, and medially where the bone suturally meets the frontal, is a narrow ventral shelf. The external surface of the dermosphenotic displays projections, depressions and lateral line pits; a lateral line canal extends

anteriorly from the pterotic into the dermosphenotic where it divides with one branch running medially into the frontal and the other extending ventrolaterally into the dorsal postorbital. Internally, the sphenotic is firmly attached to the posterior part of the dermosphenotic.

Discussion. -- The dermosphenotic of Kindleia resembles that of Amia, but in Kindleia, the bone is narrower at its posterior end, and the medial shelf that underlies the frontal is wider. Estes (1964:30) did not identify a dermosphenotic, but from the edge of the frontal he suggested that the dermosphenotic was small and oval as in Amia. The dermosphenotic of Kindleia contributes more to the posterior rim of the orbit than the same bone in Amia (if the presence of supraorbitals in Kindleia is neglected, as suggested by Estes, 1964:36).

NASAL

Specimens examined. -- None.

Illustration. -- Fig. 8.

Discussion. -- Estes (1964:30; fig. 18:38) noted that the nasal of Kindleia is virtually identical with that of Amia. Certainly the size of the premaxilla of Kindleia in the sample from the Edmonton Formation suggests that the roofing nasal is similar in size to the modern counterpart. In Amia, the nasal is a small, irregularly elliptical bone, separated posteriorly from the frontal by the parethmoid. Anteriorly, the nasal suturally meets the rostral, and laterally the adnasal. A lateral line canal extends anteroposteriorly along the middle of the nasal with two short branches, one lateral and one medial to the main canal.

ADNASAL (antorbital, Allis, 1897, Estes, 1964)

Specimens examined.-- None.

Illustration.-- Fig. 8.

Discussion.-- In 1964:30, Estes noted; "no (adnasals = antorbitals, Estes) have been identified from the University of California Lance Formation collection, but an unnumbered specimen from the Hell Creek Formation of Montana (= Lance Formation) in the Princeton University collections closely resembles that of Amia." The adnasal of Amia is a small, tear-shaped bone between the nasal and lacrimal. Externally, the adnasal is ornamented and has a few pits; internally, it is smooth, with a median ridge.

ROSTRAL (ethmoid, Allis, 1897, Goodrich, 1930; supraethmoid, Norden, 1961)

Specimens examined.-- None.

Illustration.-- Fig. 9.

Discussion.-- The rostral of Kindleia has not been identified, but in Amia, it is a small, thin, nearly Y-shaped bone resting between the anterior rim of the premaxilla below and the nasals, with which it forms a suture, above and behind.

PREMAXILLA

Specimens examined.-- UA 5405, incomplete right; UA 5439, single outer tooth; UA 5456, nearly complete right; UA 5481, incomplete right.

Illustrations.-- Fig. 10; Plate II, Fig. 2; Plate IV, Fig. 2; Plate V, Fig. 2.

Description. -- The nearly rectangular premaxilla tapers slightly posteriorly where it is suturally affixed to the internal surface of the anterior part of the frontal. Anteriorly at the margin of the jaw, the premaxilla bears a single row of elongate, posteriorly curved, conical teeth; dorsally are the roofing rostral and nasal. The periphery of the premaxilla inclines ventrally toward a large, central, olfactory foramen. The external surface of the bone is relatively smooth except for faint ribs on the posterior part.

Discussion. --The premaxillae of Kindleia and Amia resemble one another closely. Estes (1964:31), from broken material, saw no significant differences in the bone between the two genera. In Kindleia, however, the teeth seem slightly more robust, and in UA 5456, the olfactory foramen appears slightly larger and the width of the bone slightly greater (not tapering as much posteriorly) than the premaxilla of Amia. Anterior to the olfactory foramen of Amia are two small foramina, not preserved in the fossils, for the passage of C.N. VII (Janot, 1967, pl. 1, fig. 3).

MAXILLA (maxillary, Allis, 1897)

Specimens examined. -- UA 5398, left posterior end; UA 5423, posterior half of left; UA 5429, middle part of right; UA 5439, nearly complete left; UA 5450, anterior part of right; UA 5466, anterior part of right; UA 5478, anterior part of right; UA 5481, anterior part of right; UA 5505, complete right; UA 5507, middle part of left.

Measurements. -- Length, about 31 mm.; width, about 6 mm.; approximate number of teeth, 25.

Illustrations.-- Fig. 11; Plate II, Fig. 1; Plate III, Fig. 1; Plate IV, Fig. 2; Plate V, Fig. 2.

Description. -- The spatula-shaped maxilla, rod-like anteriorly and fan-shaped posteriorly, forms most of the dorsal margin to the gape. Anteriorly, the bone curves medially and forms an anteromedial process that articulates with the anterointernal surface of the premaxilla. The posterior edge of the maxilla is free (although in actinopterygians with a 'free' maxilla, ligaments connect the maxilla to the lower jaw, Schaeffer and Rosen, 1961:196) and gently convex posteriorly, but a rod-like posterior projection of the tooth-bearing edge is present ventrally. The dorsal edge of the maxilla is free anteriorly, but when the mouth is closed, the edge abuts against the ventral edge of the lacrimal; posteriorly, is a prominent supramaxillary notch. Ventrally, numerous small, conical teeth are aligned in a single, marginal row between the anteromedial process and the posterior end of the bone. The external surface fo the maxilla is lightly ornamented. The relatively smooth internal surface shows two foramina approximately two-thirds the distance from the posterior end, one slightly larger than and in front of the other. Two fossae also occur internally, one dorsally on the anteromedial process, the other on the ventral rim of the maxilla below the foramina.

Discussion. -- The maxialla of Kindleia resembles that of Amia in shape, size and degree of ossification, and in size and shape of the teeth; it differs in the depth of the anterior part of the supramaxillary notch. Estes (1964:31) reported that the notch is larger in Kindleia, but I found that differences in the dorsoventral width of the maxillae between Kindleia and Amia are slight; the excavation at the anterior edge of the notch is perhaps more extensive and the width of the bone immediately in front of the notch is perhaps greater in Kindleia, because of the

greater anterior width of the supramaxilla than in Amia. The foramina for the passage of the maxillary branch of C.N. V (Allis, 1897, fig. 29) vary in position in Amia; their pattern is relatively more constant in the fossils examined. In Amia, the anterior fossa is the point of origin of the levator maxillae muscle; the posterior fossa is the place of insertion of the superficial part of the adductor mandibularis muscle (Allis, 1897, figs. 30, 31). The similarity between these fossae in Kindleia and Amia suggest that the origin or insertion of muscles on the maxilla is very much alike in both genera.

SUPRAMAXILLA (jugal, Allis, 1897, de Beer, 1937)

Specimens examined. -- UA 5398, posterior end of left; UA 5423, posterior end of left; UA 5439, complete left; UA 5507, middle part of left.

Measurements. -- Length, about 5 mm.; width, about 3 mm.

Illustrations. -- Fig. 11; Plate V, Fig. 2.

Description. -- The supramaxilla is small, relatively elongate, and nearly biconvex with a more curved dorsal than ventral edge. The anterior margin of the bone is rounded both dorsally and ventrally from the middle; the posterior edge is rounded dorsally only and is somewhat angular ventrally. The dorsal margin of the supramaxilla is free, but when the mouth is closed, the margin adjoins the ventral edges of the suborbitals and the anterior part of the ventral postorbital. Ventrally, the supramaxilla fits into a notch of the maxilla resulting in the dorsal margin of the two bones in articulation being fairly straight. The surface of the supramaxilla is lightly ornamented externally and smooth internally.

Discussion. -- The more heavily ossified, roughly biconvex supramaxilla of Kindleia is more rounded anteriorly and posteriorly, and is wider anteriorly than

the more wedge-shaped bone of Amia. Estes (1964:31) assumed that because the supramaxillary notch was larger in Kindleia, the supramaxilla (of which he had no specimens) was also larger. I found the width of supramaxilla of Kindleia and Amia to be approximately equal (except at the anterior end of the notch). The differences in the supramaxillary notch are related to the differences in the shape of the bone in each genus, that is, as the anterior part of the supramaxilla is wider in Kindleia, then the anterior part of the notch (in order to accommodate the supramaxilla) is also wider.

LACRIMAL (preorbital, Berg, 1940; lacrymal, Norden, 1961)

Specimens examined. -- UA 5429, complete left (internal view).

Measurements. -- Length, 12 mm.; width, 8 mm.

Illustrations. -- Fig. 12.

Description. -- The small, slightly oval lacrimal shields the anterolateral part of the skull between the orbit and the maxilla. In life, the anterior margin and the dorsal margin, which is excavated posteriorly, probably were connected by cartilage to the maxilla in front and the adnasal above. The posterior edge of the lacrimal forms a suture with the anterior edge of the anterior suborbital; the ventral margin of the lacrimal is free, although it rests against the maxilla when the mouth is closed. Internally, a lateral line canal runs anteroposteriorly through the middle of the lacrimal; on each side of the canal are numerous foramina for the passage of the superior maxillary branch of C.N. V (Allis, 1897, fig. 30).

Discussion. -- The lacrimal of Kindleia (as Estes remarked, 1964:30) conforms closely in size and shape with, but is relatively heavier than, that of Amia. The excavation on the dorsal edge of the lacrimal is somewhat deeper in

Kindleia producing a slightly narrower posterior margin for contact with the anterior suborbital (roughly as shown by Estes, 1964, fig. 18b) than in Amia. This difference suggests that the anterior part of the anterior suborbital of Kindleia was narrower than the same part of Amia.

ANTERIOR SUBORBITAL (first suborbital, Allis, 1897; suborbital, Goodrich, 1930, Estes, 1964)

Specimens examined. -- None.

Illustrations. -- Fig. 12.

Discussion. -- The widths of the posterior surface of the lacrimal, which makes contact with the anterior suborbital, and the anterior edge of the posterior suborbital indicate that the anterior suborbital of Kindleia is small and thin (as Estes noted, 1964:30), but with a narrower anterior width than the same bone of Amia.

The anterior suborbital of Amia is wedge-shaped, wide anteriorly where it meets the lacrimal and narrow posteriorly where it meets the posterior suborbital. The dorsal edge of the bone forms part of the ventral margin to the orbit; the ventral edge is free. Externally, the bone is rugose with an anteroposterior line of pits extending from the lacrimal to the posterior suborbital; internally the anterior suborbital is relatively smooth.

POSTERIOR SUBORBITAL (second suborbital, Allis, 1897; suborbital, Goodrich, 1930, Estes, 1964).

Specimens examined. -- UA 5423, complete left.

Illustrations. -- Fig. 12.

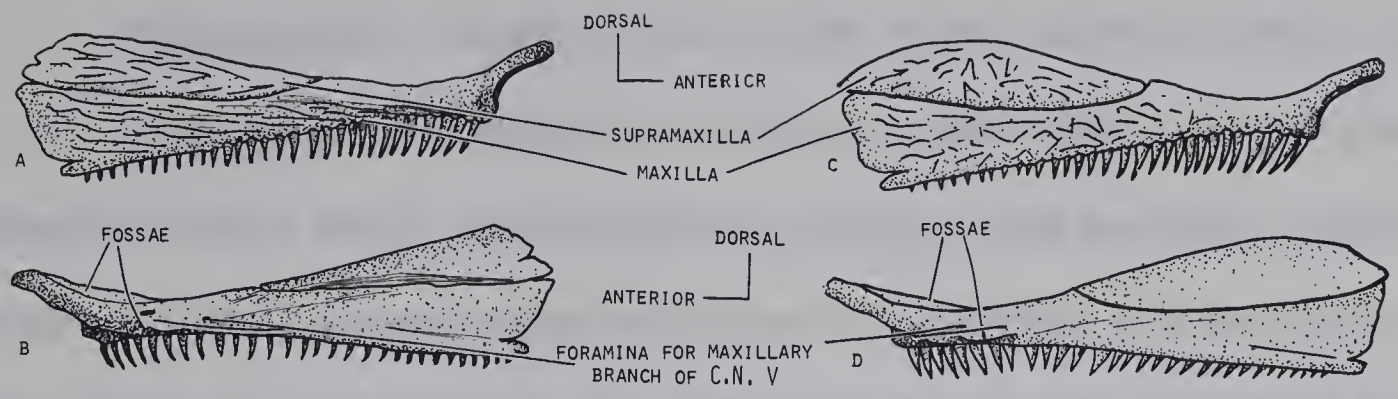


FIG. 11. MAXILLAE AND SUPRAMAXILLAE: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

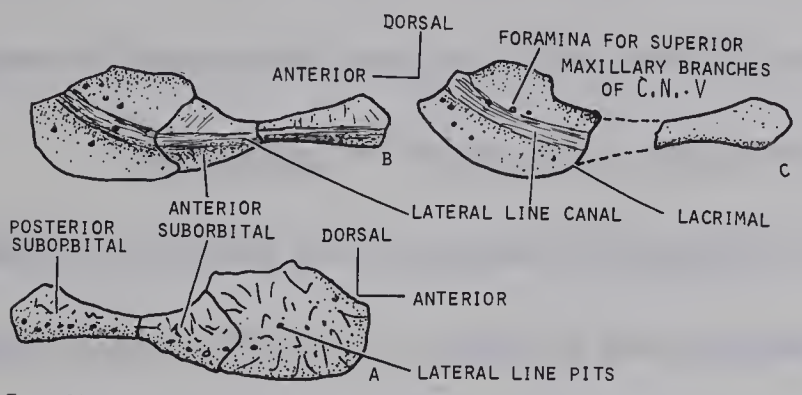
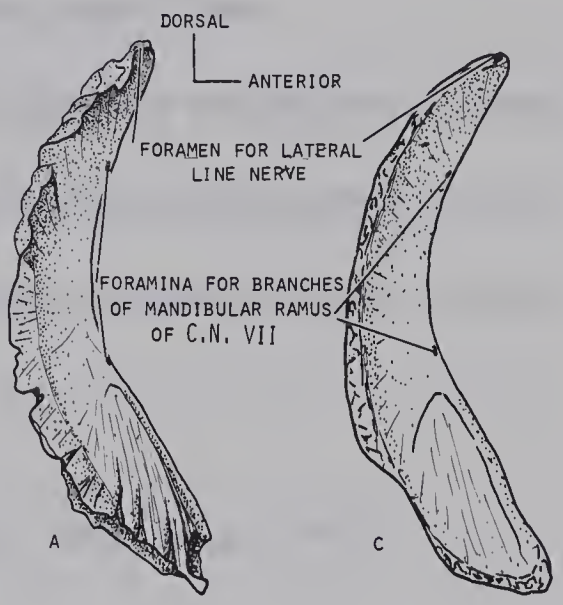


FIG. 12. LACRIMALS, ANTERIOR AND POSTERIOR SUBORBITALS: A, B, AMIA; C, KINDLEIA; A, EXTERNAL SIDE OF RIGHT; B, C, INTERNAL SIDE OF RIGHT.



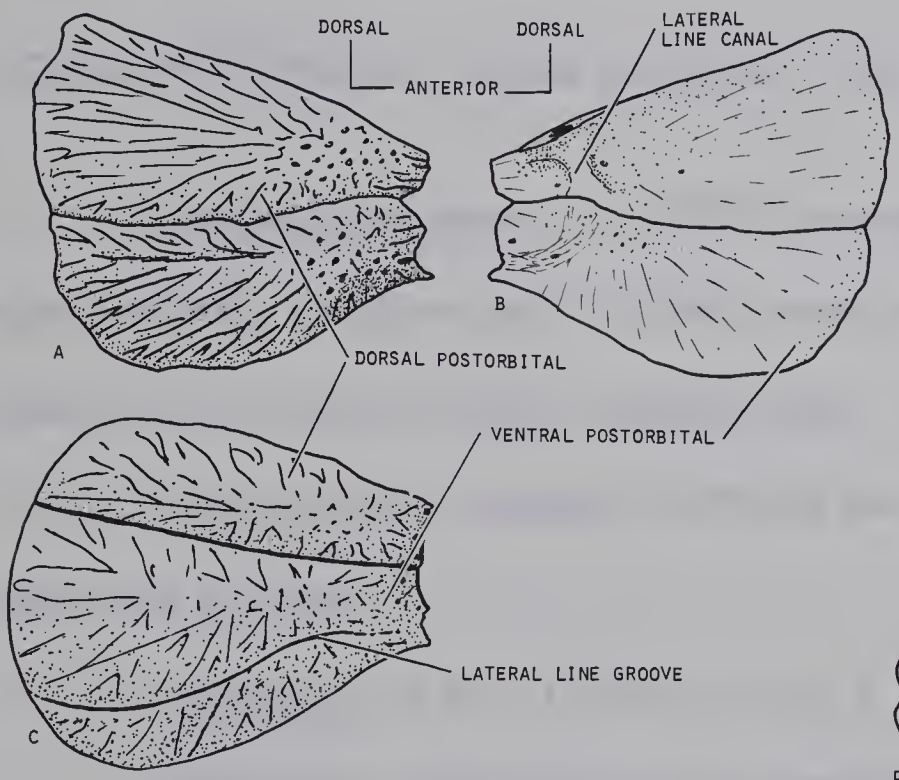


FIG. 13. DORSAL AND VENTRAL POSTORBITALS: A, B, AMIA; C, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.

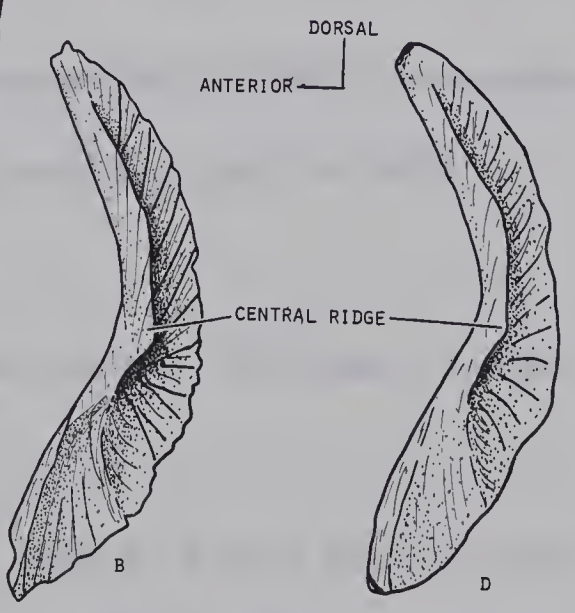


FIG. 14. PREOPERCULA: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

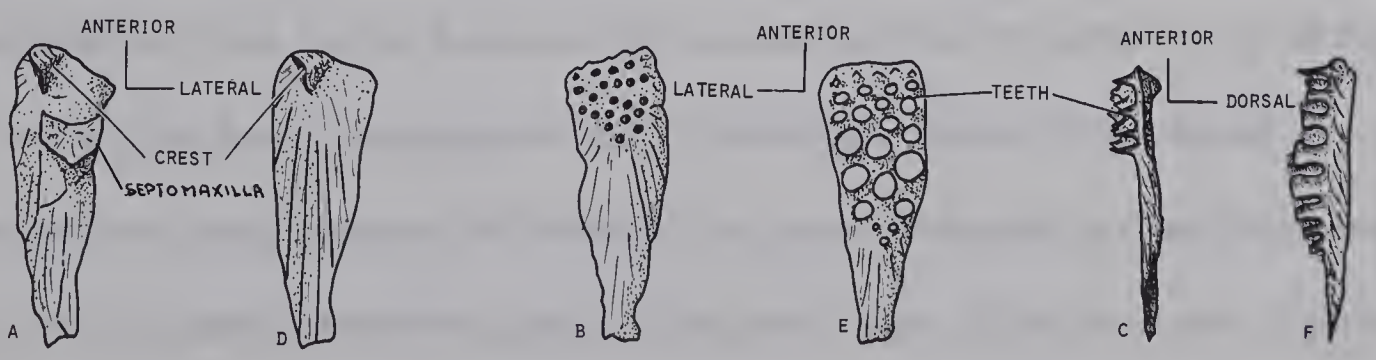


FIG. 15. VOMERS: A, B, C, AMIA; D, E, F, KINDLEIA; A, D, DORSAL VIEW; B, E, PALATAL VIEW; C, F, SIDE VIEW.

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

Measurements. -- Length, 10 mm.; width, 4 mm.; minimum width, 2.5 mm.

Description. -- The posterior suborbital is a rather small, somewhat club-shaped bone that is narrow anteriorly where it suturally meets the anterior suborbital; the bone is slightly expanded posteriorly where it interdigitates with the anterior margin of the ventral postorbital. The dorsal edge of the posterior suborbital forms a part of the ventral margin of the orbit; the ventral edge is free.

Discussion. -- The posterior suborbitals of Kindleia and Amia are virtually identical, except that the bone of Kindleia is slightly more robust anteriorly (as Estes showed, 1964, fig. 18b) and less prominently sculptured externally than the posterior suborbital of Amia.

DORSAL POSTORBITAL (second postorbital, Allis, 1897, Estes, 1964)

Specimens examined. -- UA 5398, incomplete left; UA 5426, incomplete right; UA 5480, complete right; UA 5492, nearly complete right; UA 5493, anterior part of right; UA 5505, complete right.

Measurements. -- Length, 18-28 (22) mm.; width, 7-9 (8) mm.; minimum width, 6-7 (6.5) mm.

Illustrations. -- Fig. 13; Plate I, Fig. 1; Plate II, Fig. 3; Plate III, Fig. 1.

Description. -- The flat, nearly rectangular dorsal postorbital is elongate anteroposteriorly and narrow dorsoventrally extending from the posterior rim of the orbit to (but free from) the preoperculum. The anterior margin of the dorsal postorbital is slightly concave for the orbit; the posterior margin is slightly convex, with a well rounded posterodorsal edge. The dorsal edge of the bone abuts tightly against (and was probably attached by cartilage to) the lateral margin of the roof of the skull; the edge is excavated anteriorly for the curved and downturned lateral

edge of the dermosphenotic. Ventrally, the dorsal postorbital forms a relatively straight suture with the ventral postorbital. The external surface of the dorsal postorbital carries a system of grooves and ridges that radiate from a point anterior of the center; a few large pits occur along the anterior margin. A lateral line canal extends dorsoventrally across the anterior quarter of the bone from the dermosphenotic above to the ventral postorbital below.

Discussion. -- The dorsal postorbital of Kindleia, which is the smaller of the two postorbitals, is approximately rectangular; in Amia, the dorsal postorbital is the larger of the two and is more nearly wedge-shaped with a minimum width, which is less than in Kindleia, anteriorly. Also, the posterior width of the bone is less in Kindleia than in Amia (as shown by Estes, 1964, fig. 18). On the dorsal postorbital of Kindleia, small pits are aligned in a more or less, distinct row along the anterior margin; in Amia, these external pits are placed more randomly over the anterior quarter of the bone. The dorsal postorbitals in both genera hug the lateral edge of the roof of the skull, but in Amia, there is usually a narrow, cartilage-filled gap between the dermosphenotic and the anterior part of the dorsal postorbital; this feature is probably a result of the narrowing in Amia of the anterior end of the dorsal postorbital.

VENTRAL POSTORBITAL (first postorbital, Allis, 1897, Estes, 1964)

Specimens examined. -- UA 5398, complete left; UA 5426, incomplete right; UA 5480, complete right; UA 5489, posterior fragment of left; UA 5499, nearly complete left; UA 5505, incomplete right.

Measurements. -- Length, 23-29 (24.5)mm.; width, 15-20 (17) mm.; minimum width, 4-6 (5) mm.

Illustrations. -- Fig. 13; Plate I, Fig. 1; Plate II, Fig. 3; Plate III, Fig. 1.

Description. -- The relatively flat, ventral postorbital is somewhat triangular, narrowest anteriorly and widest posteriorly. The slightly concave anterior margin dorsally forms part of the posterior rim of the orbit and ventrally interdigitates with the posterior suborbital; the convex posterior margin is concentric with (but free from) the anterior margin of the preoperculum behind. The dorsal edge of the ventral postorbital, which is suturally united with the dorsal postorbital, is nearly straight; the ventral edge, which curves upward anteriorly, is free. Externally on the postorbital, ridges radiate outward from a point anterior to the center. A lateral line canal enters the anterior quarter of the bone from the dorsal postorbital above, and it then curves anteriorly into the posterior suborbital. Also, a lateral line groove extends in a compressed S - curve from the ventral part of the above canal backward to near the posteroventral edge of the ventral postorbital; a short, ventral branch occurs about halfway along the length of the bone. The main groove divides the ventral postorbital into a lower third and an upper two-thirds. Internally, the surface of the bone is nearly smooth.

Discussion. -- The anterior part of the ventral postorbital, including the lateral line system, is closely similar in Kindleia and Amia. Posteriorly, however, the bone is expanded in Kindleia in comparison to that of Amia (as Estes remarked, 1964:31); the maximum dorsoventral width is 1.5-2 times greater in Kindleia than in Amia. The anteroposterior lateral line groove and the ventral branch appear deeper in the larger specimens of Kindleia; in Amia, they are more variable in pattern and depth than in Kindleia (although none are as distinct as in the fossils), ranging in pattern from that shown by Estes (1964, fig. 18a) to that seen in Kindleia. The inner surface of the ventral postorbital of Amia, but not of Kindleia, is pierced

by a single or numerous small foramina (probably for the accessory branches of C.N. V, Allis, 1897, fig. 29) in the anterior part. The total width of the articulated postorbitals is greater in Kindleia. In Amia, the maximum width of the dorsal postorbital is equal to or wider than the maximum width of the ventral postorbital; in Kindleia, the ventral postorbital is approximately one-third wider than the dorsal postorbital. The anterior width of the postorbitals, which is greater in Kindleia, suggests that the eye of Kindleia was larger than that of Amia.

PREOPERCULUM (opercular, Goodrich, 1930)

Specimens examined. -- UA 5398, complete left; UA 5416, incomplete left; UA 5432, fragment; UA 5452, fragment; UA 5458, incomplete left; UA 5459, nearly complete right; UA 5480, complete right; UA 5507, nearly complete left.

Measurements. -- Length, 8-9 (8.5) mm.; width, 36-42 (39) mm.

Illustrations. -- Fig. 14; Plate I, Fig. 1, Fig. 2; Plate II, Fig. 3.

Description. -- The arcuate preoperculum forms the posterior border of the palatoquadrate chamber. It extends from (but is not sutured to) the roof margin down to (but free from) the posterior border of the lower jaw. The preoperculum overlies the posterior part of the hyomandibular and symplectic and the anterior edge of the opercular series; the bone is twisted slightly so that its ventral third approximately parallels the side of the body, and the dorsal two-thirds slopes anteromedially. Crests and pits ornament the external surface of the ventral and posterior edges. At least two small foramina roughly in the middle of the bone probably carried branches of the mandibular ramus of C.N. VII (Allis, 1897, fig. 31). A lateral line canal extends through the preoperculum from the pterotic dorsally to the angular anteroventrally. Internally, the dorsal half of the preoperculum

supports a prominent, posteriorly directed, central ridge against which the anterior edge of the sub- and interopercula articulate. The inner surface posterior to the ridge and crest is slightly depressed.

Discussion. -- The only observed difference between the preopercula of Kindleia and Amia is that in Amia the posterior edge is less straight, although considerable variation in the ornamentation or smoothness of the ventral and posterior edges is seen in both genera; the degree of ornamentation seems to increase with an increase in the size of the preoperculum. Estes (1964:33) noted no differences between the preopercula of the two genera; he did, however, depict (fig. 18) a slight difference in the length of the ventral part of the preoperculum between Kindleia and Amia.

The external surface of the preoperculum provides the origin for the adductor mandibularis muscle, the biting muscle of the lower jaw (Allis, 1897, fig. 29). The resemblances between the preopercula of Kindleia and Amia suggest that the size of the adductor mandibularis was not greatly different in the two genera and that the biting power might have been comparable in both.

Ossifications of the Palatal Complex

VOMER

Specimens examined. -- UA 5402, nearly complete left and right; UA 5404, anterior part of left and right; UA 5406, nearly complete left and right; UA 5420, nearly complete right; UA 5428, incomplete left; UA 5444, numerous fragments; UA 5453, nearly complete right; UA 5461, incomplete left, UA 5481, incomplete right; UA 5488, incomplete right; UA 5494, complete left and right; UA 5504,

complete left and right; UA 5506, complete left and right.

Measurements.-- Length, 10-17 (13) mm.; width, 4-7 (5.5) mm.; approximate number of teeth, 25.

Illustrations.-- Fig. 15; Plate III, Fig. 1, Fig. 2; Plate V, Fig. 1, Fig. 3.

Description.-- The nearly triangular vomer forming the anteromedial roof of the palate is near or against (and in life was probably connected by cartilage to) the premaxilla in front and the anterior palatine and the anterior part of the entopterygoid laterally. The front part of the medial edge of the vomer interdigitates with the other member of the pair; more posteriorly, the bone tapers and diverges from the midline exposing there the anteromedial flange of the parasphenoid, with which the vomer is suturally united. The external (dorsal) surface of the vomer is slightly concave downward; at the anteromedial corner is a short crest at the base of which is a small, posterior foramen probably for the anterior palatine branch of C.N. VII (Allis, 1897, fig. 61). Posteriorly where the vomer underlies part of the parasphenoid, the external surface is rugose. Teeth are present on the anterior two-thirds of the palatal surface of the vomer; anteriorly, the teeth are small, sharply pointed and conical, but posteriorly (except for the extreme posterior few) they gradually become larger and more peg-like with broad flattened apices.

Discussion.-- The vomer of Kindleia is much like that of Amia, but is seemingly more highly ossified and definitely carries more teeth. In Kindleia, the teeth extend over the anterior two-thirds of the vomer, while in Amia they are limited to the anterior third of the bone. Almost all the vomerine teeth of Amia are sharply concial, but only the anterior row includes concial teeth in Kindleia; the remainder are blunt and peg-like. The differences between the vomers of Amia and Kindleia noted here were recorded by Estes (1964:32), as well.

ANTERIOR DERMOPALATINE (dermopalatine, Allis, 1897, Estes, 1964; palatine, Goodrich, 1930)

Specimens examined. -- UA 5406, complete left and right; UA 5457, complete left; UA 5481, complete right; UA 5494, complete right; UA 5504, complete left and right; UA 5506, complete left and right, UA 5507, complete left.

Measurements. -- Length, 6-8 (7) mm.; width, 5-6 (5.5) mm.; approximate number of teeth, 24.

Illustrations. -- Fig. 16; Plate III, Fig. 1, Fig. 2; Plate IV, Fig. 2; Plate V, Fig. 1.

Description. -- The anterior dermopalatine forms the anterolateral part of the palatal roof; there the bone is somewhat triangular with a relatively angular apex directed anteriorly to just behind (but not attached to) the premaxilla. Posteriorly, a short posteromedial flange of the anterior dermopalatine overlaps the entopterygoid; more laterally, the bone is connected by suture with the posterior dermopalatine. Along the anterior-most part of the medial edge, the anterior dermopalatine is separated from the vomer by a narrow gap, probably cartilage-filled in life. The slightly rugose, external surface holds a deep, central depression in which part of the anterior division of the superior levator maxillae muscle likely inserted (Allis, 1897, fig. 64). The walls of the depression are steep medially and laterally and gently sloped posteriorly, and in the center of the depression are a number of small foramina for the passage of anterior palatine branches of C.N. VII (Allis, 1897, fig. 62). Teeth, conical laterally, peg-shaped medially and increasing in size posteromedially, are distributed over the palatal surface of the bone.

Discussion. -- The anterior dermopalatine of Kindleia is slightly shorter (as Estes noted, 1964:32) and more highly ossified than that of Amia. The external depression is seemingly nearer the lateral edge in Amia; consequently its lateral slope is steeper and its medial slope more gentle. On the anterior dermopalatine of Kindleia, the teeth increase in size posteromedially; the anterior and lateral marginal teeth are sharp and conical, and the more medial teeth are blunt and peg-like. In Amia, most of the teeth are conical, and they increase in size posterolaterally. Nearly all other features of the anterior dermopalatine are alike in the two genera.

POSTERIOR DERMOPALATINE (dermopalatine, Allis, 1897, Estes, 1964; palatine, Goodrich, 1930)

Specimens examined. -- UA 5406, complete left; UA 5481, complete right; UA 5494, complete right; UA 5504, nearly complete left and right; UA 5506, nearly complete left and right; UA 5507, complete left.

Measurements. -- Length, 6 mm.; width, 3-5 (4.5) mm.; approximate number of teeth, 25.

Illustrations. -- Fig. 17; Plate III, Fig. 1, Fig. 2; Plate IV, Fig. 2; Plate V, Fig. 1.

Description. -- The nearly square posterior dermopalatine, inclined slightly anteromedially along the lateral margin of the palatal roof, makes sutural contact with the anterior dermopalatine anteriorly, the ectopterygoid posteriorly and the entopterygoid medially. Laterally at the edge of the palate, the posterior dermopalatine is slightly thickened to form a thin dorsal ridge or rim. Teeth on the palatal surface are long, concial and pointed in the lateral row; the teeth of the

remaining three or four rows are blunt, peg-shaped and are progressively larger posteromedially.

Discussion. -- The posterior dermopalatine of Kindleia is wider and bears more teeth in more rows (three or four according to Estes, 1964:32) than in Amia; the dermopalatine in the Recent genus carries a single row of sharp, conical, inwardly curved teeth.

ECTOPTERYGOID

Specimens examined. -- UA 5430, left fragment; UA 5453, anterior part of left; UA 5494, anterior part of right; UA 5506, center part of palatal surface visible; UA 5507, anterior part of left.

Illustrations. -- Fig. 18; Plate IV, Fig. 2.

Description. -- The anterior half (that part seen in the material collected) of the rather thin ectopterygoid tapers anteriorly at the posterolateral margin of the palate and interdigitates with the posterior dermopalatine. Laterally, the ectopterygoid is thickened and bears a row of sharp, conical, ventrally directed teeth that decrease in size posteriorly; medially, the bone overlies and is suturally united with the entopterygoid. The external surface of the ectopterygoid is relatively smooth; on the palatal surface (except at the lateral margin), are numerous, closely spaced, minute, blunt teeth.

Discussion. -- The anterior part of the ectopterygoid of Kindleia is very similar to the comparable part of the ectopterygoid of Amia, except the minute teeth that cover the palatal surface are stout and blunt in Kindleia and short and conical in Amia. Estes (1964:32) noted that the entire bone was much alike in the two genera. The entire bone of Amia (and also probably of Kindleia) is roughly

planoconvex with the posterior part forming a suture with the metapterygoid medially and with the quadrate laterally.

ENTOPTERYGOID

Specimens examined.-- UA 5481, anterior part of right; UA 5494, anterior half of right; UA 5505, posterior half of left, palatal view; UA 5507, anterior part of left.

Illustrations.-- Fig. 19; Plate III, Fig. 1; Plate IV, Fig. 2.

Description.-- The thin, triangular entopterygoid roofing the posteromedial part of the palate narrows anteriorly almost to a point, and widens posteriorly where it is probably joined by suture with the metapterygoid. The anterior part of the lateral margin of the entopterygoid overlaps and interlocks with the posteromedial edges of the two dermopalatines; more posteriorly the lateral edge interdigitates with the ectopterygoid. A narrow gap that before death was probably filled with cartilage separates the entopterygoid from the medial parasphenoid. The external surface of the entopterygoid is smooth; the palatal surface bears numerous, minute, blunt teeth.

Discussion.-- The entopterygoids of Kindleia and Amia are essentially alike, but for the shape of the minute teeth. Those in Kindleia are slightly columnar and flat-crowned, while in Amia the teeth are short and conical with blunt apices. Estes (1964:32) stated: "the principle difference between the entopterygoids of Amia calva and Kindleia fragosa is the stout articulation for the ectethmoid, which indicates that the latter was more extensive than in the Recent species, reaching almost to the lower border of the entopterygoid rather than just touching its dorsal border." Entopterygoids from the Edmonton Formation are too

poorly preserved to add to Estes' observations.

METAPTERYGOID

Specimens examined.-- UA 5416, central part of left.

Illustrations.-- Fig. 20; Plate I, Fig. 2.

Description.-- The single, incomplete metapterygoid is oriented nearly parallel to the side of the skull, and is thin and almost semi-circular, forming the extreme posterolateral wall of the palate. The anterior part of the bone is not preserved, but the posterior part seemingly overlaps the anteroventral edge of the hyomandibular. Dorsally, a deep central notch for the passage of branches of C.N. V (Allis, 1897, fig. 30) separates an anterior flange (basal process, Goodrich, 1930:406, Stensio, 1935:22, Estes, 1964:31) that is bent medially (and probably was connected by suture with the entopterygoid anteriorly) from a shorter, posterodorsal process (otic process, ibid) that in life probably served internally for insertion of part of the levator arcus palatini muscle (Allis, 1897, fig. 30). Ventrally, the metapterygoid is firmly joined with the quadrate (and probably also, when complete, with the ectopterygoid anteroventrally). The external surface of the metapterygoid bears fine radial striations or thickenings that add support to the bone.

Discussion.-- The metapterygoid from the Edmonton Formation is poorly ossified, but appears like the corresponding part of the metapterygoid of Amia. Estes (1964:31) noted also that his incomplete specimen of the metapterygoid of Kindleia resembled closely that of Amia, even to the presence of numerous, minute teeth on the palatal surface. Probably these minute teeth were blunter in Kindleia than those of Amia, as are similar teeth on the other palatal bones.

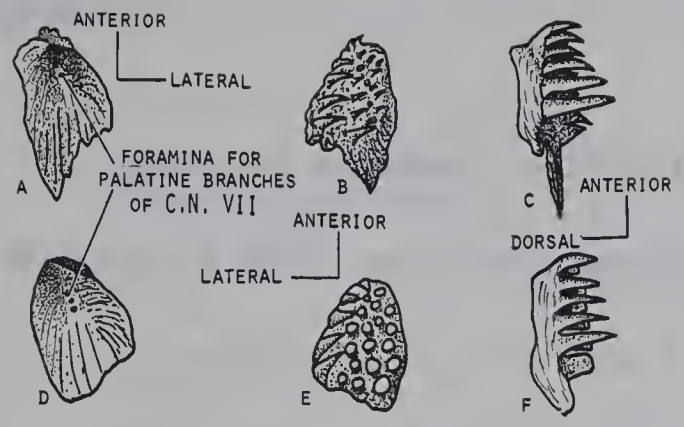


FIG. 16. ANTERIOR DERMOPALATINES: A, B, C, AMIA; D, E, F, KINDLEIA; A, D, DORSAL VIEW; B, E, PALATAL VIEW; C, F, SIDE VIEW.

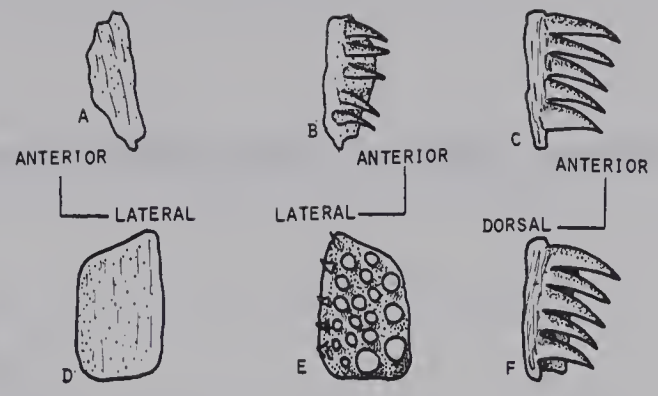


FIG. 17. POSTERIOR DERMOPALATINES: A, B, C, AMIA; D, E, F, KINDLEIA; A, D, DORSAL VIEW; B, E, PALATAL VIEW; C, F, SIDE VIEW.

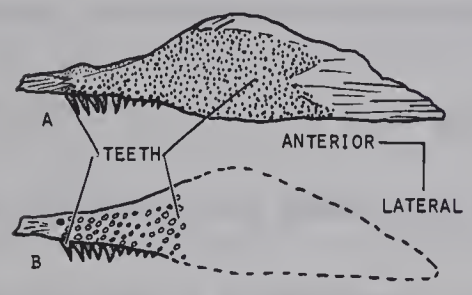


FIG. 18. ECTOPTERYGOIDS: A, AMIA, B, KINDLEIA, PALATAL VIEW OF RIGHT.

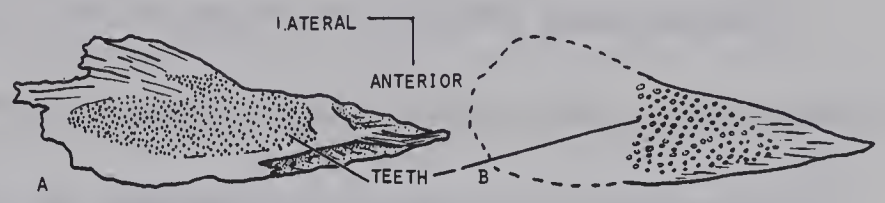


FIG. 19. ENTOPTERYGOIDS: A, AMIA, B, KINDLEIA, PALATAL VIEW OF RIGHT.

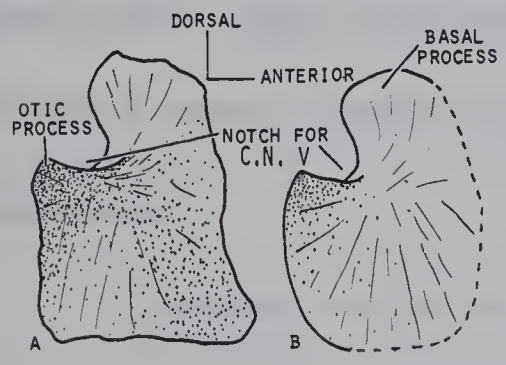


FIG. 20. METAPTERYGOIDS: A, AMIA, B, KINDLEIA, EXTERNAL SIDE OF RIGHT.

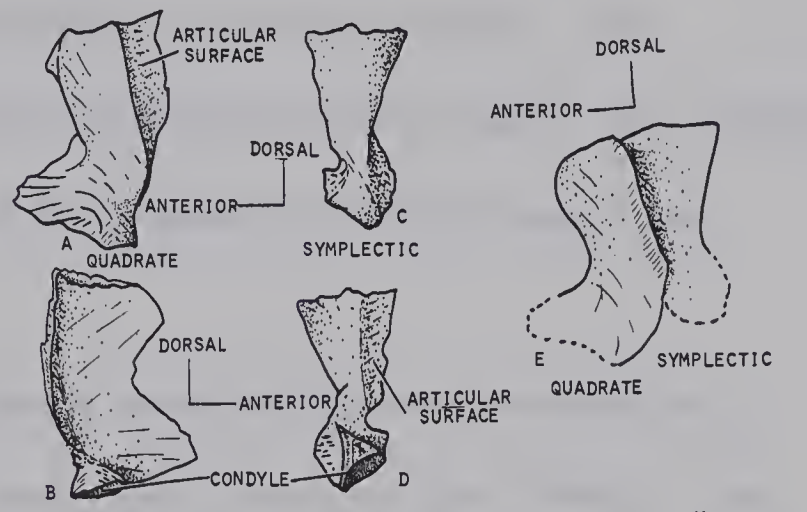


FIG. 21. QUADRATES AND SYMPLECTICS: A, B, C, D, AMIA; E, KINDLEIA; A, C, E, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

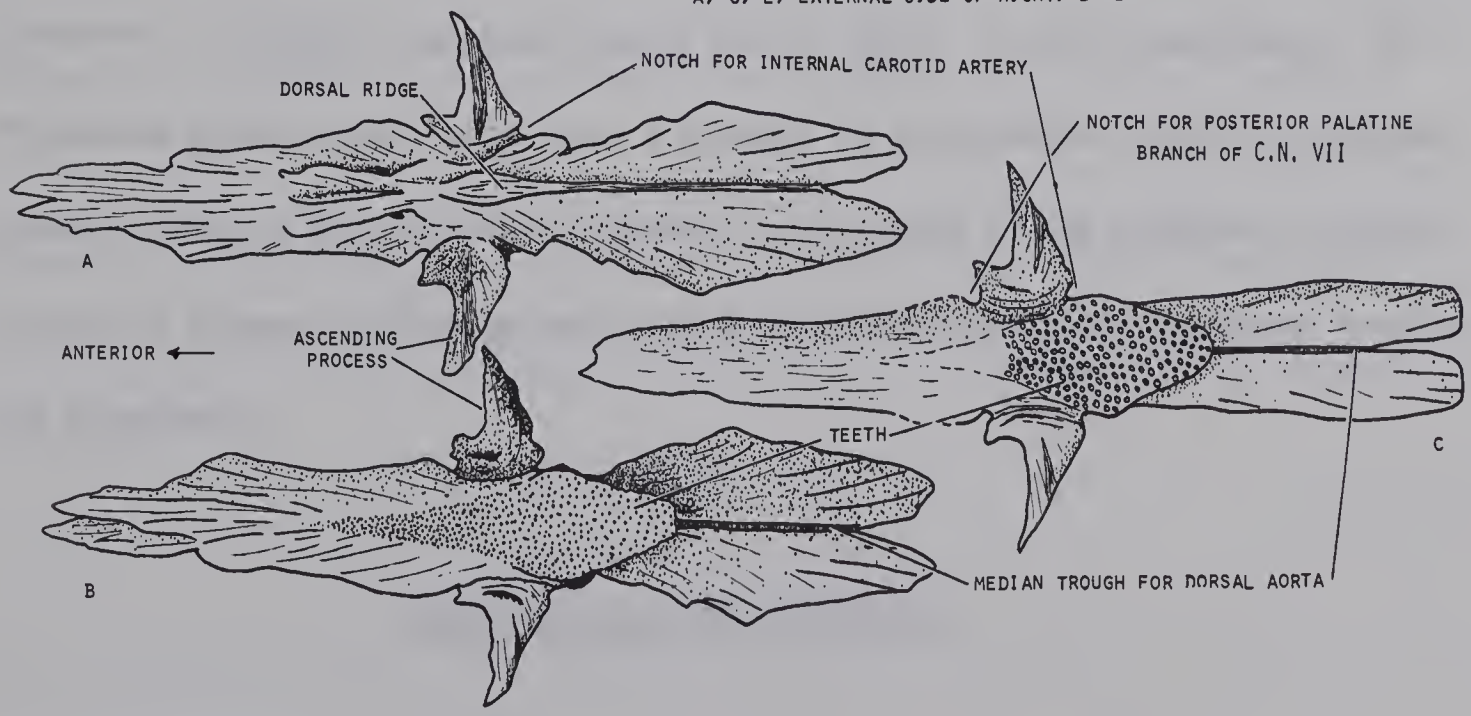


FIG. 22. PARASPHENOIDS: A, B, AMIA; C, KINDLEIA; A, DORSAL SIDE; B, C, VENTRAL SIDE.

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

QUADRATE

Specimens examined. -- UA 5416, posterior tip of left; UA 5480, posterior tip of right; UA 5507, nearly complete left.

Illustrations. -- Fig. 21; Plate I, Fig. 2.

Description. -- The thin quadrate appears somewhat L-shaped with its shorter arm directed anterodorsally and its longer arm directed posterodorsally. The bone is in sutural contact with the metapterygoid anterodorsally, and probably also (although not preserved) with the ectopterygoid anteriorly; anteroventrally, the quadrate is thickened in its articulation with the articular bone. The posteroventral edge of the quadrate that overlaps the anterior edge of the symplectic produces a narrow, lateral flange that abuts against the anterior edge of the preoperculum.

Discussion. -- On the few, poorly preserved quadrates available only the external surface is accessable to study, and as noted by Estes (1964:31), the quadrate of Kindleia resembles closely that of Amia. In the Recent genus, the thickened anteroventral edge forms a condyle for articulation with the indented posterior edge of the articular; internally, the surface of the quadrate is smooth, except for a long, shallow posteroventral indentation where the quadrate overlaps the symplectic.

Ossifications of the Braincase

PARASPHENOID

Specimens examined. -- UA 5402, anterior part; UA 5436, median part;

UA 5483, posterior flanges; UA 5504, nearly complete; UA 5505, ascending process; UA 5506, nearly complete.

Measurements. -- Length, 45-60 (52.5) mm.; width, 7-12 (9.5)mm.

Illustrations. -- Fig. 22; Plate III, Fig. 1, Fig. 2; Plate V, Fig. 3; Plate VI, Fig. 1.

Description. -- The unpaired and cross-shaped, medial parasphenoid is elongate anteroposteriorly, narrow laterally and compressed dorsoventrally; it sheaths most of the ventral surface of the chondrocranium. Anteriorly, a flange of the parasphenoid overlaps and interdigitates with the vomers; posteriorly, two flanges separated by a V-shaped excavation underlie the length of the basioccipital. Near the longitudinal center of the parasphenoid are two, long, lateral ascending processes that taper dorsally and attach to the ventrolateral part of the sphenotic; the process holds an inner transverse groove that perhaps carried the efferent pseudobranchial artery (Allis, 1897, fig. 61) and "lead into the spiracular canal" (Stensio, 1935:15). Ventrally, the ascending process bears a short anterodorsally directed flange that appears to fit under and support the Gasserian ganglion (Allis, 1897, fig. 63). At the base of the entire process, are small anterior and posterior notches that hold the posterior palatine branch of C.N. VII and the internal carotid artery, respectively (ibid, fig. 61). A distinct dorsal ridge extends along the midline over the middle third of the external surface of the parasphenoid. Internally, numerous minute, blunt teeth are distributed on the central third of the bone; these are followed in the posterior third by a deep median trough that houses the dorsal aorta (ibid, fig. 63).

Discussion. -- The parasphenoid of Kindleia and Amia conform in size and shape, but in Kindleia the bone is more highly ossified, is thicker dorsoventrally

and more ventrally convex below. Estes (1964:29) noted these differences, but in addition, he stated that in Kindleia the extent of the tooth-bearing surface carried further laterally than in Amia. Evidence among the specimens from the Edmonton Formation fails to substantiate that difference. However, other differences are evident: (1) the posterior flanges of the parasphenoid are more rounded and less tapered posteriorly, and they underlie the entire length of the basioccipital; in Amia, they are more angular and fail to reach the posterior edge of the basioccipital. (2) The dorsal median ridge is slightly higher in Kindleia than in Amia, and as in Amia, it probably fits into a groove in the cartilaginous ethmoid and the interorbital septum (Norden, 1961:702). (3) The tiny ventral teeth are blunt, rather than sharply conical as in Amia.

In the Recent genus, as well as probably in Kindleia (although not preserved in the specimens available), near the center of the base of the ascending process and along the sides of the anterior part of the dorsal ridge, are foramina that carry palatal branches of C.N. VII (Allis, 1897, figs. 17, 61).

BASIOCCIPITAL

Specimens examined.-- UA 5483, nearly complete; UA 5506, essentially complete.

Measurements.-- Length, 13 mm.; width, 9-11 (10) mm.; thickness, 4-5 (4.5) mm.

Illustrations.-- Fig. 23; Plate III, Fig. 1, Fig. 2; Plate VI, Fig. 1.

Description.-- The semi-cylindrical basioccipital forms the posterior floor of the chondrocranium; posteriorly, the bone is slightly concave and oval in cross section where it articulates with the first vertebral centrum. The internal

surface of the basioccipital is weakly rugose and convex downward, and except for the posterior half of a deep, medial, longitudinal groove, the internal surface of the bone is sheathed by the posterior flanges of the parasphenoid. The medial groove contains near its posterior rim a pair of foramina for exit of the intervertebral artery and sympathetic nerve (Allis, 1897, fig. 10), and also posterior to these, are a pair of shallow depressions where the ventral, cartilaginous occipital processes of the aortal supports attached (ibid, fig. 15). The relatively wide lateral sides of the basioccipital bear near their posterior limits a depression that holds a large foramen for the entrance of the intervertebral artery and sympathetic nerve (Allis, 1897, fig. 10).

Discussion. -- Only two specimens of the basioccipital of Kindleia were collected, neither of which lent itself to the study of its dorsal features. The basioccipital of Kindleia is much like that in comparable parts of Amia, but for slight differences in shape and length. The basioccipital in Amia is only gently tapered posteriorly, but more so than in Kindleia, in which the sides are essentially parallel. In Amia, the bone is longer and not sheathed to its full, posterior extent by the parasphenoid. The lateral and ventral foramina and the single pair of ventral depressions are nearer to the posterior edge in Kindleia; in Amia, the foramina and the anterior pair of the two sets of ventral depressions are placed more anteriorly, opposite or anterior to the posterior limit of the flanges of the parasphenoid.

Estes (1964:29) noted that the excavation in the external surface of the basioccipital is less deep in Kindleia than in Amia, and that in Amia the excavated area is filled with fatty tissue. Estes also suggested that the greater length of the basioccipital and the presence of a second pair of ventral depressions

in Amia indicate that the "basioccipital posterior to the spinal (intervertebral) arterial foramina includes only one fused vertebra (in Kindleia) instead of the two found in A. calva (Allis, 1897:706)". This difference might mean that the basioccipital of Kindleia is more primitive than that of Amia, and that in the Recent genus the skull has become lengthened by the addition of a vertebra, thereby increasing the arc of rotation of the head as expressed at its anterior end.

OPISTHOTIC (intercalar, Stensio, 1935; intercalary, Berg, 1940)

Specimens examined. -- UA 5506, complete left.

Measurements. -- Length, 15 mm.; width, 14 mm.

Illustrations. -- Fig. 24; Plate III, Fig. 2.

Description. -- The thin, poorly ossified, somewhat triangular opisthotic of the posterodorsal region of the chondrocranium is inclined ventromedially. The bone has anterolateral, posterior and medial edges, as well as a distinct posterolateral, thickened and indented apex for articulation with the end of the anteroventral process of the suprascapular. The anterolateral and posterior edges of the opisthotic are slightly arched forward, and each curves dorsally producing a flange; the dorsal flange of the anterolateral edge overlaps the external surface of the ventral flange of the pterotic, and that of the posterior edge movably articulates with the epiotic. The medial edge of the opisthotic bears three short processes (anteromedial, medial and posteromedial) separated by two notches; the articulations of these processes are not preserved in the specimen available, but according to Goodrich (1930, fig. 300), the anteromedial process articulates with the prootic, the medial process with the basioccipital and the posteromedial process with the exoccipital.

Discussion. -- In Kindleia, ossification of the opisthotic is more nearly complete than in Amia; the anteromedial and posteromedial processes of the bone apparently extend more medially in Kindleia than in Amia, suggesting possibly a firmer articulation of the opisthotic with the surrounding bones in Kindleia. In other features, the opisthotics of Kindleia and Amia are very similar.

SPHENOTIC (postorbital ossification, Allis, 1897; postfrontal, Goodrich, 1930; autosphenotic, Stensio, 1935)

Specimens examined. -- UA 5398, nearly complete left; UA 5416, incomplete left; UA 5456, incomplete right; UA 5505, essentially complete left.

Illustrations. -- Fig. 24; Plate I, Fig. 1, Fig. 2.

Description. -- The sphenotic is small and tetrahedral, with one side firmly attached to the ventral surface of the posterior part of the dermosphenotic and the anterior part of the pterotic, and a second surface is almost parallel to the side of the skull. The lateral part of the ventral apex immovably receives the dorsal end of the ascending process of the parasphenoid.

Discussion. -- The sphenotic conforms closely in size and shape between Kindleia and Amia, although it is better ossified in Kindleia, likely giving greater support to the ascending process of the parasphenoid.

Ossifications of the Opercular Series and the Ventral Surface of the Skull

OPERCULUM (opercular, Goodrich, 1930)

Specimens examined. -- UA 5398, incomplete left; UA 5416, incomplete left; UA 5421, anterior half of left; UA 5422, incomplete right; UA 5441,

fragment; UA 5447, dorsal part of left; UA 5452, incomplete left; UA 5455, incomplete left; UA 5464, fragment; UA 5465, fragment of left; UA 5474, incomplete left; UA 5480, nearly complete right; UA 5482, incomplete left; UA 5489, dorsal half of left; UA 5504, nearly complete left; UA 5505, incomplete left; UA 5507, nearly complete left.

Measurements.-- Length, 24-29 (26.5) mm.; width, 24-29 (27) mm.

Illustrations.-- Fig. 26; Plate I, Fig. 1, Fig. 2; Plate II, Fig. 3; Plate III, Fig. 1.

Description.-- The flat operculum, the dorsal-most bone of the opercular series, is nearly square but for the rounded corners. The bone thins posteroventrally from a maximum thickness at its anterodorsal corner. Anteriorly, the edge of the operculum articulates movably with the internal ridge of the preoperculum; also, a crescent-shaped ridge on the anterodorsal part of the internal surface of the operculum bears an anterior facet for articulation with the opercular process of the hyomandibular. Posteriorly, the edge of the operculum is free. The dorsal edge of the bone abuts against (but is not joined to) the suprascapular; the ventral edge has a narrow notch anteriorly for an anterodorsal projection of the subopercular, while the rest of the edge overlaps onto a dorsal shelf of the subopercular. The external surface of the operculum is prominently ornamented, except for a narrow strip along the anterior and dorsal edges where the bone curves slightly medially. The internal surface of the bone is relatively smooth, but the anterodorsal ridge displays numerous, ventral foramina probably for opercular branches of C.N. VII (Allis, 1897, fig. 29).

Discussion.-- The opercula of Kindleia and Amia differ in shape, with the operculum of Kindleia more nearly "quadrate" (Estes, 1964:33) than in Amia.

The maximum length of the bone of Kindleia occurs about midway along its width; in Amia, the maximum length is more ventral. Also in Kindleia, the posterior edge is more nearly vertical, while in Amia, the posterior edge slants anterodorsally so that its dorsal edge is shorter and its posterior edge more arched than in Kindleia. The angle of the posterodorsal corner approximates 90° in Kindleia, and not the 120° of Amia. As well, in Kindleia the anterodorsal corner is more rounded than in Amia.

The opercula from the Edmonton Formation are slightly more rounded posterodorsally and posteroventrally and more nearly equidimentional than those studied by Estes (1964, figs. 16e, 18b).

The dissimilarity in shape between the opercula of Kindleia and Amia suggest differences in the pattern of musculature associated with these bones. The adductor operculi, which arises from the lateral edge of the pterotic and inserts, in part, on the dorsal and posterodorsal edges of the operculum, and the levator and dialotor operculi, both of which arises on the ventrolateral surface of the pterotic and insert, in part, on the anterior and anterodorsal edges of the operculum, were perhaps longer in Kindleia in order to reach the posterior part of the longer dorsal edge and the more rounded anterodorsal corner of the operculum. Longer muscles in Kindleia implies their more oblique angle of insertion on the operculum than in Amia, and possibly then, their less forceful effect when contracted. Of greater significance, however, is the place of insertion of these muscles with respect to the point of pivot of the operculum on the opercular process of the hyomandibular. The levator and dilator operculi insert slightly more posterior to the ventral facet than in Amia, and thereby with contraction of these muscles, the swing of the posterior part of the operculum is more dorsolateral, than

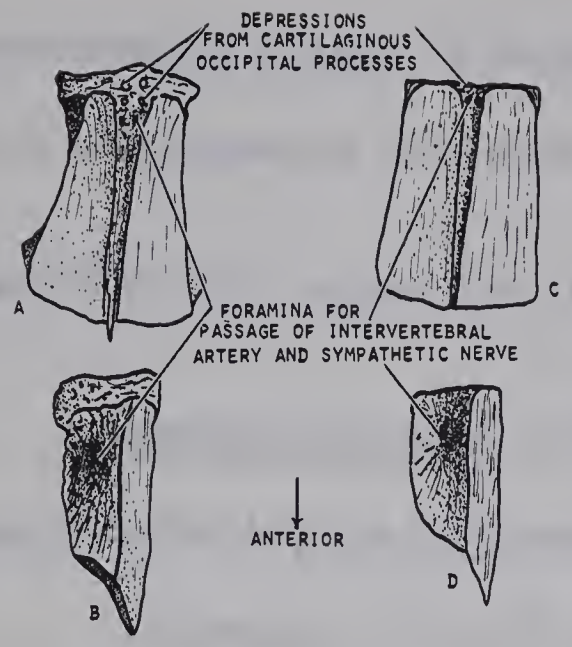


FIG. 23. BASIOCCIPITALS: A, B, AMIA; C, D, KINDLEIA; A, C, VENTRAL VIEW; B, D, SIDE VIEW.

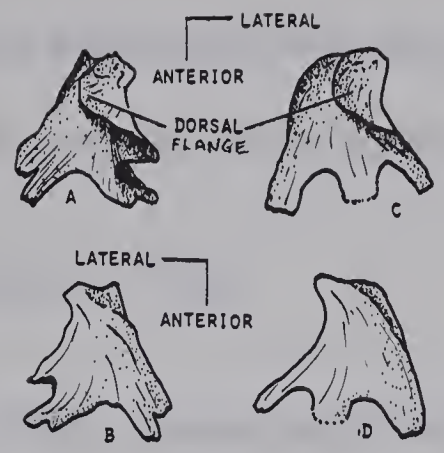


FIG. 24. OPISTHOTICS: A, B, AMIA; C, D, KINDLEIA; A, C, DORSAL VIEW OF RIGHT; B, D, VENTRAL SIDE OF RIGHT.

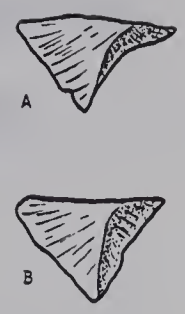


FIG. 25. SPHENOTICS: A, AMIA, B, KINDLEIA, LATERAL SIDE OF RIGHT.

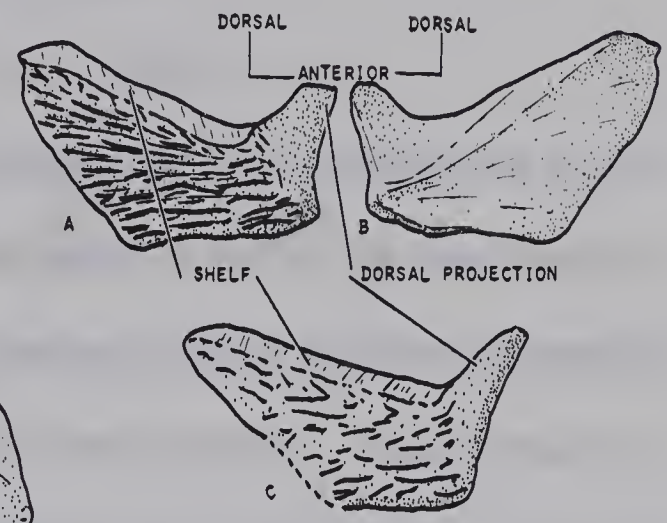


FIG. 27. SUBOPERCULA: A, B, AMIA; C, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.

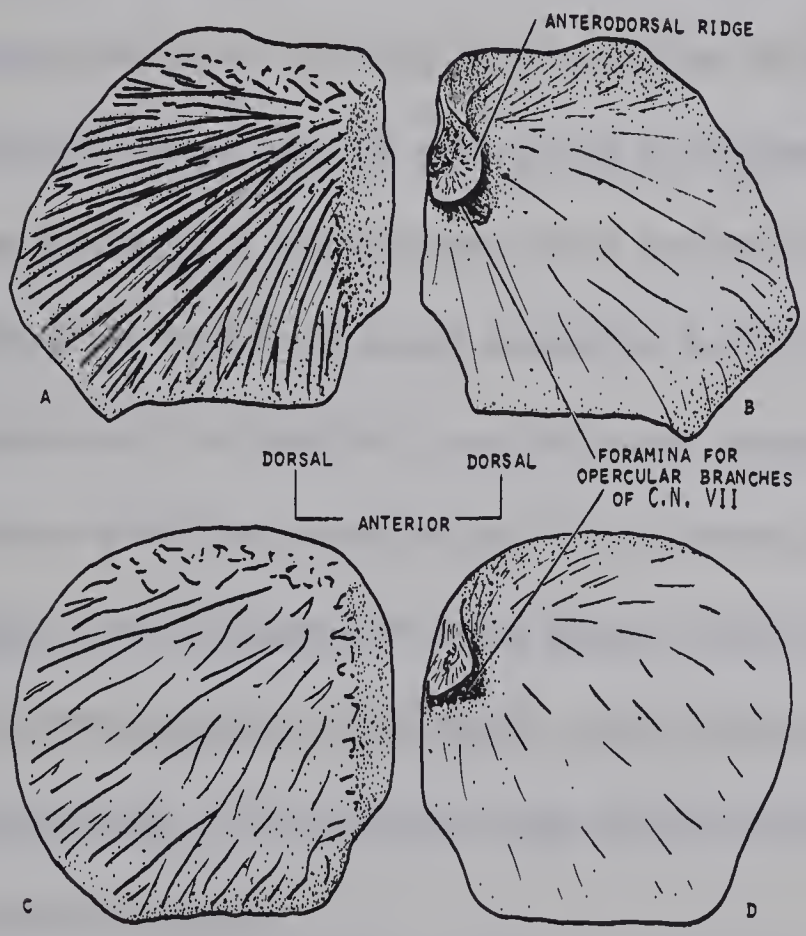


FIG. 26. OPERCULA: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; D, E, INTERNAL SIDE OF RIGHT.

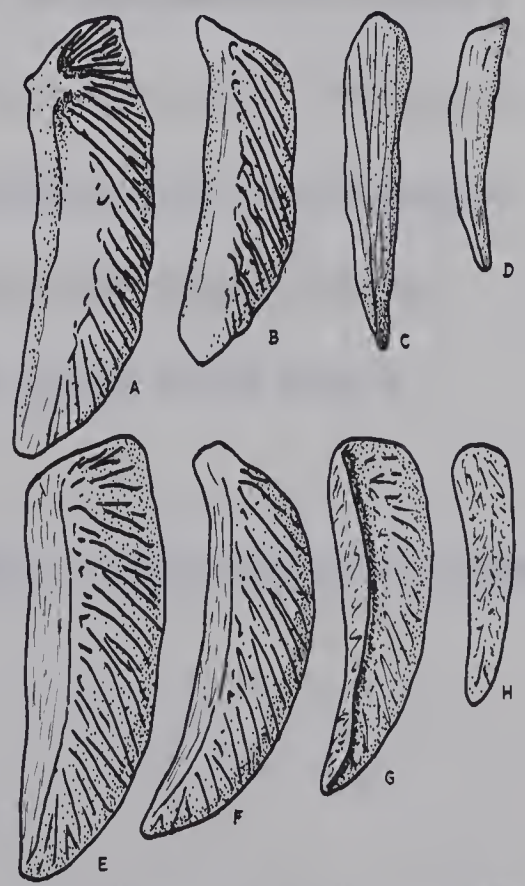


FIG. 29. BRANCHIOSTEGAL RAYS: A, B, C, D, AMIA; E, F, G, H, KINDLEIA; A, E, EXTERNAL SIDE OF DORSAL-MOST RAY; B, F, EXTERNAL SIDE OF SECOND FROM DORSAL-MOST RAY; C, G, EXTERNAL SIDE OF RAY FROM NEAR MIDDLE OF SERIES; D, H, EXTERNAL SIDE OF MORE VENTRAL RAY.

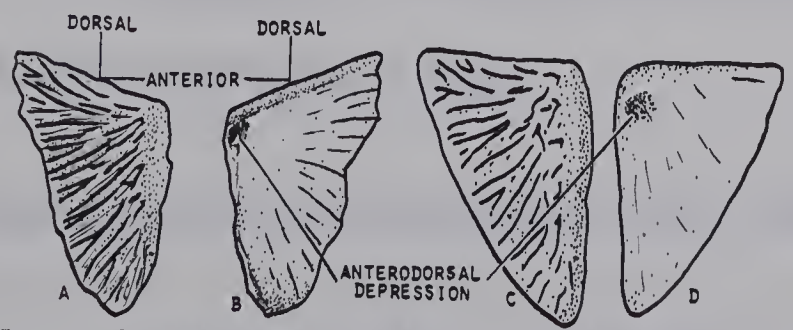


FIG. 28. INTEROPERCULA; A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

anterolateral as in Amia. If the above difference is real then Kindleia likely could not increase the aperture of its opercular slit as widely as Amia.

SUBOPERCULUM (subopercular, Goodrich, 1930)

Specimens examined.-- UA 5398, anterior part of left; UA 5416, anterior half of left; UA 5485, anterior part of left.

Illustrations.-- Fig. 27; Plate I, Fig. 1, Fig. 2.

Description.-- The thin, broad suboperculum is the middle bone in the opercular series. Anteriorly, it underlies the posterior half of the preoperculum and articulates with the ventral part of the internal ridge of that bone; posteriorly, the free edge of the suboperculum is inclined anteroventrally. Except anteriorly where the bone has a dorsal projection that fits into an anteroventral notch of the operculum, the relatively straight dorsal margin of the suboperculum supports a narrow shelf that underlies and forms a suture with the operculum. The ventral edge of the suboperculum abuts against (and was probably held by cartilage to) the interoperculum. Externally, most of the surface of the bone is heavily ornamented, but the anterior edge and the internal surface of the bone is relatively smooth.

Discussion.-- The suboperculum of Kindleia, as Estes (1964:33) recorded, closely resembles that of Amia.

INTEROPERCULUM (interopercular, Allis, 1897)

Specimens examined.-- UA 5469, ventral half of right; UA 5487, complete right; UA 5490, ventral two-thirds of left.

Measurements.-- Length, 9 mm.; width, 15 mm.

Illustrations.-- Fig. 28.

Description.-- The approximately triangular interoperculum is ventral in the opercular series. It meets (and was probably held by cartilage to) the subopercului above, and overlaps the upper branchiostegal rays below. The smooth anterior margin of the interoperculum fits under the preoperculum; its posterior margin is inclined downward and forward to an acute, subrounded apex. Externally, the surface of the bone is ornamented; internally it is generally smooth, but does display a small anterodorsal depression for articulation with the epihyal.

Discussion.-- The interopercula of Kindleia and Amia are much alike, as Estes (1964:33) noted.

BRANCHIOSTEGAL RAYS

Specimens examined.-- UA 5401, left ventral rays; UA 5416, incomplete dorsal-most ray; UA 5419, complete left ventral ray; UA 5422, anterior half of ventral ray; UA 5435, complete left ventral ray; UA 5480, nearly complete dorsal ray; UA 5506, essentially complete left and right series of rays.

Measurements.-- Largest ray: length, 23-30 (26.5) mm.; width, 7-8 (7.5) mm. Smallest ray: length, approximately 16 mm.; width, approximately 3 mm.

Illustrations.-- Fig. 29; Plate II, Fig. 3; Plate III, Fig. 1, Fig. 2.

Description.-- The ten, well ossified, blade-like branchiostegal rays begin anteriorly about one-third along the length of the hyoid arch, with which the anterior-most end of each ray movably articulates, and extend posteriorly and dorsally over the posteroventral and posterolateral sides of the skull to just below and medial to the sub- and interopercula. Each successively more posterior ray is

slightly longer and more robust than those that precede. The dorsal-most and largest ray, truncated anteriorly and somewhat acute posteriorly, bears a fairly straight dorsal margin and a ventral margin that curves downward and forward. The next, more ventral branchiostegal ray is nearly banana-shaped; the anterior end tapers and curves dorsally, and the almost angular posterior end is rounded ventrally. The remaining eight rays are elongate, rounded distally, tapered anteriorly, and convex ventrally. Nearly the entire external surface of each ray carries posteroventrally inclined grooves and ridges; however, the dorsal three or four rays bear a narrow, smooth dorsal shelf on which the following ray overlaps and movably articulates. More anteroventrally in the branchiostegal series, the rays lack a definite shelf and instead overlap each other medioventrally. Some rays exhibit a distinct ridge between the ornamented and non-ornamented zones that forms a low buttress against which the next more dorsal ray abuts and moves.

Discussion. -- The articulated fossil, UA 5506, has ten branchiostegal rays, in comparison with the eleven or twelve in Amia. All of the rays in Kindleia are more highly ossified and more extensively ornamented. The dorsal-most ray (as Estes, 1964:33, mentioned) and the smallest few are shaped much alike in the two genera, but the second largest ray is more rounded anteriorly. The remaining rays are more rounded distally than in Amia (as noted by Estes, 1964:34). The central ridge on the external surface is less constant and less distinct in Amia than in Kindleia.

The branchiostegal rays of Kindleia, although perhaps fewer in number, are slightly more robust anteriorly and therefore probably covered a comparable part of the undersurface of the throat as in Amia. The prominent external ridges

and the degree of ossification suggest that the rays of Kindleia were more rigidly intercalated and likely, in articulation, were less flexible than those of Amia.

GULAR (median gular, Goodrich, 1930)

Specimens examined. -- UA 5505, nearly complete; UA 5506, incomplete.

Measurements. -- Length, 27-38 (32.5) mm.; width, 12-22 (17) mm.

Illustrations. -- Fig. 30; Plate III, Fig. 1, Fig. 2.

Description. -- The roughly rectangular gular, ventrally convex and anteroposteriorly elongate, sheaths the undersurface of the pharyngeal cavity anterior to the branchiostegal rays. Anteriorly, the gular is rounded and tapered, and attaches (probably by cartilage) to the dentaries near their symphysis; posteriorly, the gular is squared. Fine striations radiate from the center on the external surface.

Discussion. -- The gulars of Kindleia and Amia are essentially similar in shape and size, but in Amia, the posterior edge of the gular can be either squared, as in Kindleia, or rounded. Estes (1964) lacked gulars of Kindleia in the sample available to him.

Ossifications of the Mandibular Arch

DENTARY

Specimens examined. -- UA 5398, posterior tip of left; UA 5406, anterior part of right; UA 5407, fragment of right; UA 5408, posterior part of right; UA 5411, anterior part of right; UA 5412, anterior part of right; UA 5413,

fragment of left; UA 5414, fragments; UA 5415, fragments; UA 5439, nearly complete left; UA 5446, anterior part of right; UA 5450, incomplete right; UA 5480, nearly complete right; UA 5494, anterior part of right; UA 5504, complete left and right; UA 5505, complete left and right; UA 5506, complete left and right; UA 5507, complete left.

Measurements.-- Length, 36-49 (43) mm.; width, 12-14 (13) mm.; approximate number of teeth, 15.

Illustrations.-- Fig. 13; Plate II, Fig. 3; Plate III, Fig. 1, Fig. 2; Plate V, Fig. 1, Fig. 2.

Description.-- The elongate dentary is the anterior-most and largest bone of the lower jaw. Longitudinally, the bone arches upward, and tapers and curves inward anteriorly to a ventrally rounded margin at the ligamentous symphysis; transversely, the bone bends downward and inward to an acute, free, ventromedial margin. The ventral two-thirds of the posterior edge is excavated, and there overlaps onto a long anterior shelf of the angular; the dorsal third, also slightly excavated, is united by suture with the surangular. Except for the acute dorsal edge of the posterior third of the dentary, the dorsal margin is rounded and recurved medially; on its crest the margin bears a single row of about 15 sharp, conical, posteromedially curved teeth. Externally, the surface of the dentary is slightly ornamented: it also displays an alignment of oval, lateral line pits extending from the anteroventral part of the angular upward and forward to near the dorsal edge of the dentary about one-quarter the length of the bone from the anterior end; anteriorly and slightly more ventrally are a few additional pits. Most of the internal surface of the dentary is finely striated for articulation with the more medial bones of the lower jaw or for muscular insertion. The dorsal

area, recurved and thickened, connects by cartilage with the anterior and posterior coronoids and the prearticular; ligaments of the symphysis attach at the anterointernal rim; the intermandibularis, geniohyoideus and hyohyoideus muscles insert, from front to back, respectively, along the anterior part of the ventrointernal edge, and the adductor mandibularis muscle inserts on the internal surface of the posterior half of the bone (Allis, 1897, fig. 43). Also, on the ventral part of the anterior half of the dentary are two small foramina for the passage of the internal mandibular branches of C.N. VII (Allis, 1897, fig. 44; Janot, 1967, pl. 1, fig. 1a).

Discussion. -- The dentary of Kindleia is more extensively ossified, more robust anteriorly and has a more acute ventral edge than the dentary of Amia. Estes (1964:32) noted that in Kindleia the dentary is relatively deep anteriorly, "is not prominently sculptured", has a ventral "knife edge", "posteriorly is bent ventrad" and has 14 to 17 long, inwardly curved teeth. The symphyseal edge is wider and less rounded ventrally in Kindleia than in Amia, producing a wider symphysis and a wider margin for ligamentous and cartilaginous attachment; this difference suggests that the symphysis of Kindleia was more rigid than that of Amia. The thinner ventral part of the dentary, however, is less rigid than in Amia, probably a more primitive feature in Kindleia having become altered in the evolution of Amia. The muscles that insert on this part of the dentary mainly raise the hyoid apparatus when the lower jaw is fixed by the adductor mandibularis, or depress the lower jaw when the hyoid is fixed by the hyoclavicularis (McMurrich, 1884:320). The effective power of these muscles possibly increased, with the decrease in flexibility (and likely also with the increase in surface available for muscle attachment), as the ventral part of the dentary expanded in thickness.

ANGULAR (dermarticular, Goodrich, 1930; articular, Allis, 1897, Gregory, 1933, de Beer, 1937, Berg, 1940).

Specimens examined. -- UA 5398, complete left; UA 5480, complete right; UA 5505, nearly complete left; UA 5506, complete left and right.

Measurements. -- Length, about 18 mm.; width, about 13 mm.

Illustrations. -- Fig. 32; Plate I, Fig. 1; Plate II, Fig. 3; Plate III, Fig. 1, Fig. 2.

Description. -- The angular, the posteroventral and second largest, external bone of the lower jaw, is roughly triangular. Its anterior margin slants anteroventrally and displays a long shelf that fits under the posterior part of the dentary. The free, posterior edge of the angular is truncate in the ventral quarter, excavated in the quarter above (to accommodate the symplectic when the lower jaw is dropped) and gently tapered forward in its dorsal half. Dorsally, the short margin connects by suture with the surangular; ventrally, where the angular is longest, the edge is acute. A pit line canal extends longitudinally along the ventral part of the external, ornamented surface from the free preoperculum behind to the dentary in front; a second series of pits extends along the posterior margin of the angular above the posteroventral excavation.

Discussion. -- The angular of Kindleia is generally conformable in size and shape to that of Amia (as Estes, 1964:33, noted), but the anterior shelf is wider, the anterior edge more slanted and the ventral edge more acute in Kindleia than in Amia. The internal surface of the angular is not available in the specimens collected from the Edmonton Formation. In Amia, the internal surface bears a central foramen for the external mandibular branch of C.N. VII (Allis, 1897,fig. 43; Janot, 1967, pl. 1, fig. 2a). Also, in Amia three tiny, nearly circular bones

are fused to the inner surface; these are: the coronomeckelian (ossicle d Bridge, 1877; articular, Goodrich, 1930; os Meckeli, Berg, 1940) on the posterointernal margin directly above the posterior excavation of the angular, and which has a condyle for the symplectic; the articular (ossicles b and c, Bridge, 1877, Allis, 1889) just below the central foramen that movably articulates with the quadrate, and the retroarticular (ossicle a, Bridge, 1877; angular, Goodrich, 1930) at the posteroventral end of the angular which attaches to the mandibular-hyoid ligament (Allis, 1887, fig. 2).

SURANGULAR (supra-angular, Allis, 1897, Goodrich, 1930)

Specimens examined.-- UA 5398, complete left; UA 5506, complete right.

Measurements.-- Length, about 3.5 mm.; width, about 6.5 mm.

Illustrations.-- Fig. 33; Plate I, Fig. 1; Plate III, Fig. 2.

Description.-- The surangular is small and triangular with its anterior edge connected by suture with the dentary and its ventral side interdigitating with the dorsal margin of the angular. The posterior edge of the surangular inclines anterodorsally, and is free. Externally, the surface of the bone is ornamented and exhibits a number of lateral line pits near its ventral border.

Discussion.-- In the fossil material available, only the ornamented part of the surangular is visible; it is essentially like that of Amia. In Amia (and probably in Kindleia), an anterior shelf of the surangular underlies the dentary, and a wide, smooth, posterior platform bends slightly inward forming the posterior edge of the coronoid process.

ANTERIOR CORONOID (splenial, Allis, 1897; first coronoid, Estes, 1964)

Specimens examined.-- UA 5405, complete left; UA 5439, incomplete left; UA 5445, fragments; UA 5446, nearly complete right; UA 5453, incomplete left; UA 5480, nearly complete left; UA 5494, nearly complete right; UA 5504, essentially complete left and right; UA 5505, essentially complete left and right; UA 5506, essentially complete left and right; UA 5508, complete left.

Measurements.-- Length, 8-12 (9.5) mm.; width, approximately 5 mm.; number of teeth, 10-14.

Illustrations.-- Fig. 34; Plate III, Fig. 1, Fig. 2; Plate V, Fig. 2.

Description.-- The small, slightly wedge-shaped anterior coronoid extends, and expands in width, posteriorly from the anterior edge of the internal surface of the dentary to its suture with the posterior coronoid behind. The anterior coronoid arches over the inner part of the rounded and thickened dorsal edge of the dentary, and extends downward and inward hugging the internal side of the dentary. The pharyngeal surface of the anterior coronoid bears numerous teeth of variable shape, which increase in size medially. The more lateral teeth are blunt and conical; the inner teeth are long, stout and peg-like and curve upward to form a broad tooth-plate medial to the dentary. The ventrolateral surface of the anterior coronoid is slightly rugose and in life was probably held firmly by cartilage to the dentary.

Discussion.-- The anterior coronoid of Kindleia differs from that of Amia (as Estes, 1964:33, noted) in width and in shape and size of the teeth. In Amia, the bone is slightly narrower and more dorsal and lateral than in Kindleia. All the teeth on the anterior coronoid of Amia are sharp, conical and dorsally directed, increasing in size laterally. In Kindleia, the toothed surface extends more medial and ventral,

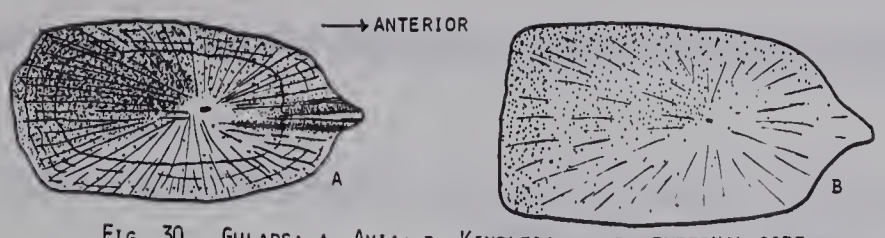


FIG. 30. GULARS: A, AMIA; B, KINDLEIA; A, B, EXTERNAL SIDE.

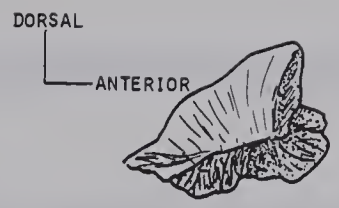


FIG. 33. SURANGULAR: AMIA (APPROXIMATELY SAME IN KINDLEIA) EXTERNAL SIDE OF RIGHT.

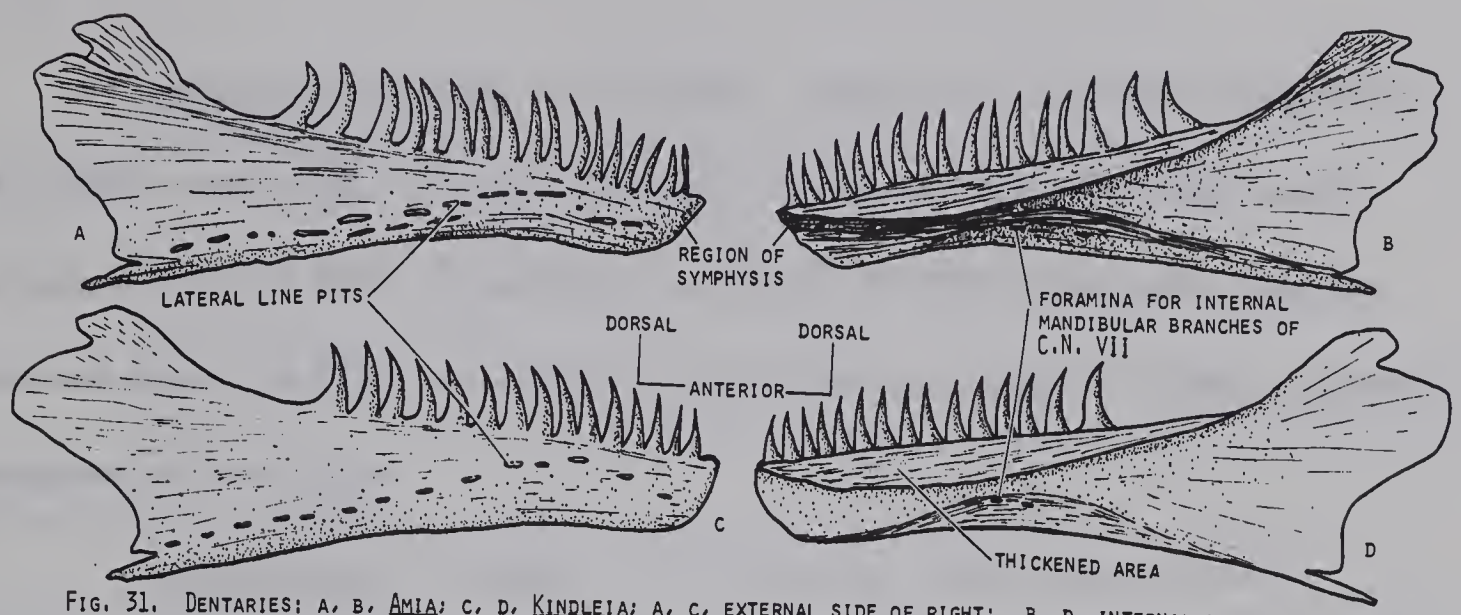


FIG. 31. DENTARIES: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

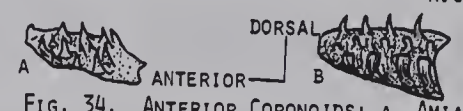


FIG. 34. ANTERIOR CORONOIDS: A, AMIA; B, KINDLEIA; A, B, PALATAL SIDE OF RIGHT.

FIG. 35. POSTERIOR CORONOIDS: A, AMIA; B, KINDLEIA; A, B, PALATAL SIDE OF RIGHT.

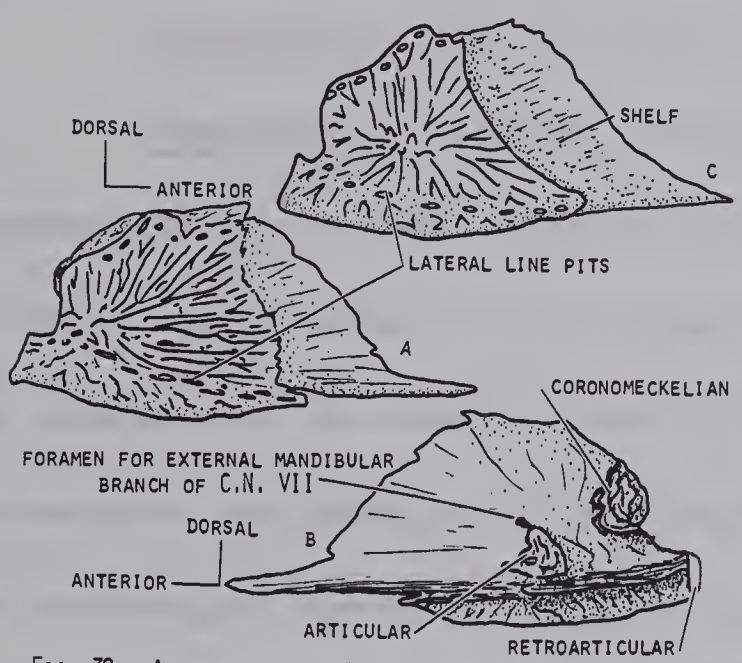


FIG. 32. ANGULARS: A, B, AMIA; C, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.

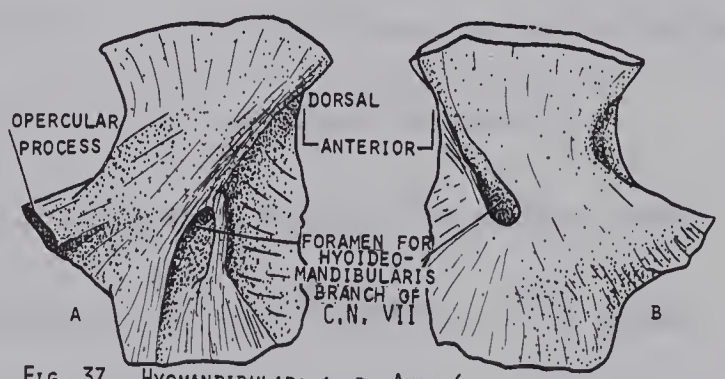


FIG. 37. HYOMANDIBULAR: A, B, AMIA (NEARLY IDENTICAL TO KINDLEIA); A, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.

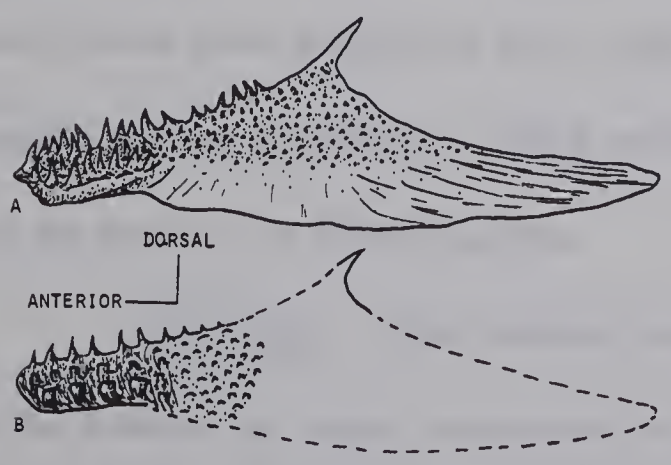


FIG. 36. PREARTICULARS: A, AMIA, B, KINDLEIA; A, B, PALATAL SIDE OF RIGHT.

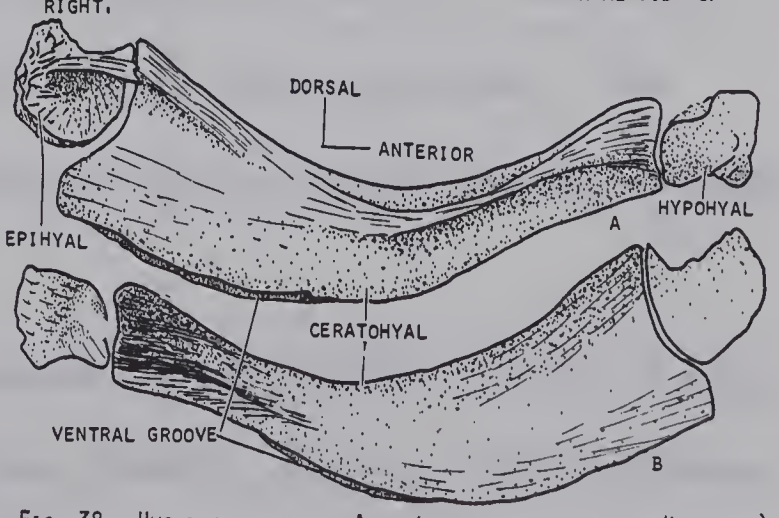


FIG. 38. HYOID ARCH: A, B, AMIA (NEARLY IDENTICAL TO KINDLEIA); A, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

and the more medial teeth are larger and more strongly curved than the outer teeth.

POSTERIOR CORONOID (splenial, Allis, 1897; anterior coronoid, Goodrich, 1930; second coronoid, Estes, 1964)

Specimens examined. -- UA 5439, complete left; UA 5445, fragments, UA 5446, anterior part of right; UA 5453, incomplete left, UA 5480, nearly complete left; UA 5494, anterior part of right; UA 5504, essentially complete left and right; UA 5505, essentially complete left and right; UA 5506, essentially complete left and right.

Measurements. -- Length, 6-10 (7.5) mm.; width, about 4 mm.

Illustrations. -- Fig. 35; Plate III, Fig. 1, Fig. 2; Plate V, Fig. 2.

Description. -- The small, rectangular posterior coronoid is elongate anteroposteriorly; its anterior edge overlaps the posterior margin of the anterior coronoid, and its posterior edge is connected by suture with the prearticular behind. In cross section, the posterior coronoid forms an asymmetrical fold with its anterodorsal third sitting on the inner part of the dorsal edge of the dentary and its ventromedial two-thirds hugging the internal side of the dentary. The upper, pharyngeal surface bears teeth, of which the lateral-most are blunt, conical and small; those more medial are stout, peg-like, large and curved dorsally. The ventral surface of the bone, which rests against (and was probably held by cartilage to) the dentary, is faintly rugose.

Discussion. -- The posterior coronoid of Kindleia differs from that of Amia in the form of the teeth, mentioned by Estes (1964:33), and in the width and shape of the bone. In Kindleia, the posterior coronoid is wider, bears more teeth, and extends more medially and ventrally than in Amia. The more labial teeth are

small, blunt and conical, and those more lingual are large and peg-like; nearly all the teeth of Amia are small and conical.

PREARTICULAR (splenial, Allis, 1897; coronoid, Goodrich 1930)

Specimens examined.-- UA 5439, anterior part of left; UA 5453, anterior part of left; UA 5468, posterodorsal tip of right.

Illustrations.-- Fig. 36.

Description.-- The limited sample of the prearticular available from the Edmonton Formation shows the bone to be thin and poorly ossified, forming the lingual surface of the lower jaw behind the coronoids. The narrow, anterior edge of the prearticular is suturally joined to the posterior coronoid in front; posteriorly, the bone is excavated and free. The dorsal edge of the prearticular curves slightly outward and downward where it meets (and was probably connected by cartilage to) the dorsal edge of the dentary. The lateral and anterior edges of the pharyngeal surface bears small, conical teeth that decrease in size posteriorly; the rest of this surface is sheathed with tiny, blunt closely spaced teeth.

Discussion.-- A complete specimen of the prearticular of Kindleia is not known among the materials from the Edmonton Formation or among those from the Lance Formation studied by Estes (1964). The broken specimens on hand, however, suggest that the prearticular in Kindleia is much like that of Amia, with that of Kindleia bearing blunter internal teeth. In Amia, the excavated posterior edge allows passage of the adductor mandibularis muscle anterolaterally, where it inserts on the internal surface of the dentary.

Ossifications of the Hyoid Arch

HYOMANDIBULAR

Specimens examined.-- UA 5401, dorsal part of left; UA 5416, complete left; UA 5482, incomplete left; UA 5507, posterior half of left.

Measurements.-- Length, 22 mm.; width at the dorsal edge, 12 mm.

Illustrations.-- Fig. 37; Plate I, Fig. 2.

Description.-- The hatchet-shaped hyomandibular is thickest and convex upward dorsally, where it movably articulates primarily in an anteroposterior plane, with the ventrolateral part of the pterotic and the posterolateral part of the sphenotic; the hyomandibular thins ventrally, and there is connected, probably by cartilage, to the posterior margin of the metapterygoid and the posterodorsal edges of the quadrate and symplectic. Most of the anterior and posterior margins are free, but a short posterior process (the opercular process) passes directly medial to the preoperculum; this process bears a terminal condyle for articulation with a facet on the anterodorsal corner of the operculum. The external surface of the hyomandibular displays a wide ridge that extends from the anterodorsal corner to the center of the bone; from here, the ridge divides into ventral and posteroventral arms on either side of a large central foramen, which carries the hyoideo-mandibularis branch of C.N. VII (Allis, 1897, fig. 31).

Discussion.-- The hyomandibulars of Kindleia and Amia are almost identical (as Estes, 1964:33, noted). In Amia (and, most likely, also in Kindleia) ligaments extend from the ventrointernal surface of the hyomandibular to the posterior and posteroventral parts of the epi- and ceratohyal (Allis, 1897, fig. 5). Also, the levator arcus palatini muscle that arises near the lateral edge of the pterotic inserts

on the external surface of the hyomandibular anterior to the wide ridge; the adductor hyomandibularis that arises from the pterotic behind the levator arcus palatini inserts on the posterior undersurface of the hyomandibular immediately above the opercular process (Allis, 1897, figs. 36, 37). These muscles were probably nearly alike in the two genera.

SYMPLECTIC

Specimens examined.-- UA 5507, nearly complete left.

Illustrations.-- Fig. 21.

Description.-- The thin, wedge-shaped symplectic tapers anteroventrally. It underlies, and in life was likely held by cartilage to, the posteroventral edge of the quadrate and the anterior edge of the ventral part of the preoperculum.

Discussion.-- The single, poorly preserved symplectic of Kindleia from the Edmonton Formation is essentially identical to that of Amia. In Kindleia (as in Amia) the anteroventral part of the symplectic is probably thickened into a socket for articulation with the rounded posterior edge of the coronomeckelian (ossicle d, Bridge, 1877). Estes (1964:31) lacked specimens of the symplectic of Kindleia.

CERATOHYAL

Specimens examined.-- UA 5438, incomplete left; UA 5480, nearly complete left and right; UA 5494, posterior half of left; UA 5504, nearly complete left; UA 5506, nearly complete right; UA 5507, posterior fragment of left.

Illustrations.-- Fig. 38; Plate II, Fig. 3; Plate III, Fig. 1, Fig. 2.

Description.-- The arcuate ceratohyal, the largest bone of the hyoid arch,

is oval in cross-section anteriorly and blade-like posteriorly. Midway along its length, the ceratohyal twists so as to incline the anterior part medially and the posterior part dorsoventrally. The bone is free but for its anterior and posterior margins that in life were probably joined by cartilage to the hypohyal and epihyal, respectively (although no fossil specimens of these two are at hand). The dorsal edge of the ceratohyal is relatively smooth and round; the ventral edge is slightly rugose for movable articulation with the anterior ends of the branchiostegal rays, and is grooved probably for passage of the hyoid branch of C.N. VII (Allis, 1897, fig. 31). Striae, which show areas of muscle attachment, occur on the external and internal surfaces of the ceratohyal; the geniohyoideus arises from the posteroventral and external surfaces of the bone and the hyohyoideus from the upper border and the internal surface (Allis, 1897, fig. 46).

Discussion.-- The ceratohyal of Kindleia and Amia are essentially alike (as Estes, 1964:31, noted). The epi- and hypohyal of Kindleia have not been recorded, either from the Edmonton Formation or from the Lance Formation, but in Amia, they are small, rounded bones held by cartilage to the ends of the ceratohyal.

Ossifications of the Pectoral Girdle and Fin

SUPRASCAPULAR (post-temporal, Goodrich, 1930, Janot, 1967)

Specimens examined.-- UA 5398, essentially complete left and right; UA 5416, complete left; UA 5433, fragment of left; UA 5442, incomplete right; UA 5467, fragments; UA 5482, essentially complete left; UA 5500, posterior half of left; UA 5506, essentially complete left.

Measurements.-- Length (at roof edge), 11-15 (13) mm.; width (measured along the posteromedial edge), 19-25 (22) mm.

Illustrations.-- Fig. 39; Plate I, Fig. 1, Fig. 2; Plate III, Fig. 1, Fig. 2.

Description.-- The wing-shaped suprascapular, the dorsal-most bone of the pectoral girdle, in part, underlies the posterior edge of the extrascapular in front. The anterior edge of the suprascapular is wide and arched posteriorly, extending from the roof edge medially and anteriorly to the midline, where it meets with the opposite bone of the suprascapular pair. The free lateral edge is nearly in line with the outer margin of the skull roof, but the free posteromedial edge slants markedly posterolaterally to a rounded, posterior apex. Except for a small patch of rugose surface on the posterolateral half of the bone, the external surface is unornamented; the anterolateral corner exhibits a large foramen for the entrance of the longitudinal lateral line canal from the extrascapular. Internally, a prominent, distally fluted, anteroventral process that movably articulates with the posterior edge of the opisthotic bears at its posterior base a large foramen for passage of the lateral line canal from the suprascapular to the supracleithrum below. Posterior to the internal foramen is an articular surface for contact with the external, anterodorsal part of the supracleithrum.

Discussion.-- The size and shape of the suprascapular of Kindleia is very similar to that of Amia (as stated by Estes, 1964:34), but the posterior apex of the bone is slightly wider and more rounded in Kindleia than in Amia.

SUPRACLEITHRUM

Specimens examined.-- UA 5398, complete left and dorsal half of right; UA 5416, essentially complete left; UA 5417, complete right; UA 5470, dorsal

tip of left; UA 5482, ventral half of right.

Measurements.-- Length, about 10 mm.; width, about 29 mm.

Illustrations.-- Fig. 40; Plate I, Fig. 1, Fig. 2.

Description.-- The roughly rectangular supracleithrum, the dorsal-most and second largest bone of the cleithral series, is elongate dorsoventrally, its length inclined posteromedially and its width posteroventrally. The free, anterior margin of the supracleithrum is thickened, and curved medially; the free, slightly convex, posterior margin is notched about midway along its width. In the dorsal quarter, the bone tapers to an upper point that runs along the ventral side of the anteroventral process of the suprascapular; ventrally, where the supracleithrum overlaps and is joined suturally to the anterodorsal part of the metacleithrum posteriorly and the dorsal tip of the cleithrum more anteriorly, the edge is truncated and posteriorly rounded. A low ridge extends posteroventrally on the external surface of the supracleithrum from an anterodorsal foramen to the posterior edge of the bone about halfway between the notch and the dorsal tip; anterior to this ridge is an articular surface that meets with the posterointernal, articular surface of the suprascapular above. Internally, the supracleithrum is concave with a prominent anterior rim; a broad ridge, housing the lateral line canal that runs from the suprascapular above to the trunk behind, intervenes between the anterodorsal foramen and the posterior notch with a second foramen. Both the inner and outer surfaces of the bone are relatively unornamented.

Discussion.-- The supracleithra of Kindleia and Amia resemble each other in size and shape, but the fossil bone is better ossified. The length of the supracleithrum of Kindleia remains constant throughout most of its width, except for the tapered dorsal end, but in Amia, the taper of the supracleithrum begins

about midway along its width and ends in a truncated dorsal edge, rather than the pointed tip of Kindleia. Estes (1964) did not identify the supracleithrum of Kindleia.

METACLEITHRUM

Specimens examined. -- UA 5398, nearly complete left; UA 5416, essentially complete left; UA 5476, complete right; UA 5501, nearly complete left.

Measurements. -- Length, 7-9 (7.5) mm.; width 14-17 (15) mm.

Illustrations. -- Fig. 41; Plate I, Fig. 1, Fig. 2.

Description. -- The well-ossified, nearly ovoid metacleithrum is the middle and smallest bone of the cleithral series. Anteriorly, the edge is slightly arched forward, underlying the posteroventral part of the supracleithrum and the posterodorsal part of the cleithrum; posteriorly, the margin is free and gently curves backward. The metacleithrum is wide and truncated dorsally; ventrally, it tapers to a somewhat acute apex that is posteriorly rounded. Externally, the bone is convex outward, and, except for the extreme anterior edge, is faintly rugose; the internal surface is smooth and featureless.

Discussion. -- The metacleithrum of Kindleia (not identified by Estes, 1964) conforms closely in size to that of Amia, but the Recent bone is more nearly bean-shaped with both anterior and posterior edges arched slightly backward and with no tapering of the bone ventrally. In Kindleia, the ventral edge is posteriorly rounded; the outer surface is slightly rugose. In Amia, the ventral edge is anteriorly rounded instead: both inner and outer surfaces are smooth.

CLEITHRUM

Specimens examined. -- UA 5416, posterior half of left; UA 5452, posterior half of left; UA 5472, fragment; UA 5473, dorsal tip of left; UA 5480, nearly complete left and right; UA 5482, fragment of right; UA 5506, complete left and right.

Measurements. -- UA 5506: length, 60 mm; width (along posterior edge) 36 mm.; width (in anterior three-quarters) 25 mm.

Illustrations. -- Fig. 42; Plate I, Fig. 2; Plate II, Fig. 3; Plate III, Fig. 1, Fig. 2.

Description. -- The relatively large, well-ossified, L-shaped cleithrum has its longer limb directed horizontally and its shorter limb directed vertically. Anteriorly, the tips of the cleithra meet at the midline; posteriorly the edges are free. Each edge is rounded posteroventrally and shows two notches in the dorsal half at the overlap with the metacleithrum. The nearly straight, dorsal margin of the longitudinal limb is thickened, bearing there a deep groove for origin of the hyopectoralis (sternohyoideus, Allis, 1897) and the external pharyngo-clavicularis muscles (McMurrich, 1884:322). In the posterior quarter of the cleithrum, the vertical limb tapers dorsally to a rod-like, fluted, dorsal tip with an anterior, thickened edge and a short dorsoventral groove impressed on its posterior edge; the dorsal half of the limb underlies the ventral part of the supracleithrum and overlies the anterior part of the metacleithrum; in life the three cleithral bones were probably flexibly joined by cartilage. The ventral edge of the cleithrum is thin, acute, free, and tapers upward anteriorly; about one-third in length from the posterior edge, the margin is notched for cartilage connecting the bone with the

pectoral fin. The external surface of the posterior part of the cleithrum is flat, lightly ornamented and parallel to the side of the skull; the anterior two-thirds is smooth, and twists inward dorsally. The internal surface of the bone is concave; about midway along the bone's length, the thickened dorsal edge curves posteroventrally as a thickened crest to near the mid-length of the bone, where it terminates in a shallow depression, likely in which the abductor muscles of the pectoral fin arose (McMurrich, 1884:322).

Discussion. -- The cleithra of Kindleia and Amia are essentially similar in size and shape, but in Kindleia, the cleithrum is more highly ossified, more prominently sculptured posteriorly, and the horizontal arm is slightly wider than that of Amia. The groove on the posterior edge of the vertical limb and the groove along the dorsal edge of the longitudinal limb in Amia (and in Kindleia) each contains a foramen for passage of a spinal nerve to the sternohyoideus and external pharyngo-clavicularis muscles (McMurrich, 1884:322).

PECTORAL FIN

Specimens examined. -- UA 5507, incomplete left; fragments and impressions.

Description. -- The fan-shaped pectoral fin, located ventrolaterally on the side of the body directly behind the dorsal-most branchiostegal ray, consists of distal fin rays that articulates with more proximal pterygiophores. The pectoral fin rays are long, paired rods expanded and divided longitudinally at their base, where each rod of the pair articulates with opposite sides of the distal end of the pterygiophore in front; distally, the fin rays are segmented and bifurcated. The pterygiophores are short, narrow shafts that gradually expand posteriorly.

Discussion. -- The pectoral fin of Kindleia (as seen in the few broken specimens) resembles that of Amia. In Amia, the fin connects by cartilage to the cleithrum in front. The pterygiophores proximally consist of a main bony shaft; distally, the bone is replaced by cartilage. The cartilage is not preserved in the sample of Kindleia collected from the Edmonton Formation, but it probably was present in Kindleia, as in Amia.

Ossifications of the Pelvic Girdle and Fin

BASIPTERYGIUM (pelvic bone, Goodrich, 1930)

Specimens examined, -- UA 5418, nearly complete right with the posterior tip missing.

Illustrations. -- Fig. 43.

Description. -- The basipterygium is flat, triangular, and posteriorly tapered. The anterior part of the ventral surface is slightly rugose; the remainder of the bone is smooth.

Discussion. -- The basipterygium of Kindleia is better ossified than in Amia. The bone in Amia is an isosceles triangle; in Kindleia, it more nearly resembles a right-angled triangle with its medial side longest. The basipterygium tapers posteriorly to an ovate shaft in Amia, but remains relatively flat and broad in Kindleia.

In Amia, the basipterygium supports four short pterygiophores (Goodrich, 1930, fig. 206). The articular surface of the basipterygium for the pterygiophores behind is thinner and wider in Kindleia, suggesting that the rays of Kindleia were more numerous or more widely spaced than in Amia.

PELVIC FIN

Specimens examined.-- A single unnumbered impression and a few possible unnumbered fragments.

Description.-- The pelvic fin is a small, fan-shaped structure positioned abdominally about midway along the body. The fin rays are short, paired rods that widen and are segmented and bifurcated distally.

Discussion.-- The pelvic fins of Kindleia and Amia appear approximately the same in size and shape. In Amia, the paired rods of each fin ray separate proximally, and articulate opposite one another with either side of the more anterior pterygiophore; the four short pterygiophores, in turn, articulate with the distal end of the basipterygium (Goodrich, 1930, fig. 206). The single pelvic fin of Kindleia available appears to be slightly wider than that of Amia, although this may be an artifact of preservation; nevertheless, the greater posterior width of the basipterygium suggests that the pelvic fin of Kindleia was slightly larger than that of Amia.

Axial Column

VERTEBRAE

Specimens examined.-- UA 5403, isolated caudal vertebra; UA 5425, posterior trunk and caudal vertebrae; UA 5440, anterior trunk vertebrae; UA 5443, anterior trunk vertebrae; UA 5448, posterior trunk and caudal vertebrae; UA 5483, anterior trunk vertebrae; UA 5502, anterior-most trunk vertebra; UA 5506, anterior trunk vertebrae.

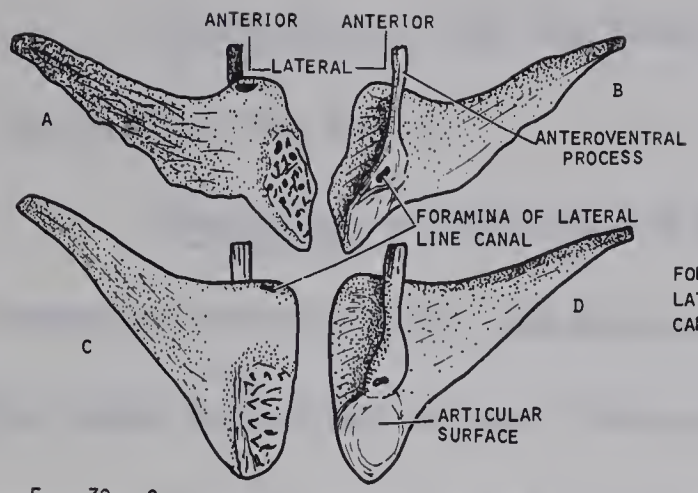


FIG. 39. SUPRASCAPULARS: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

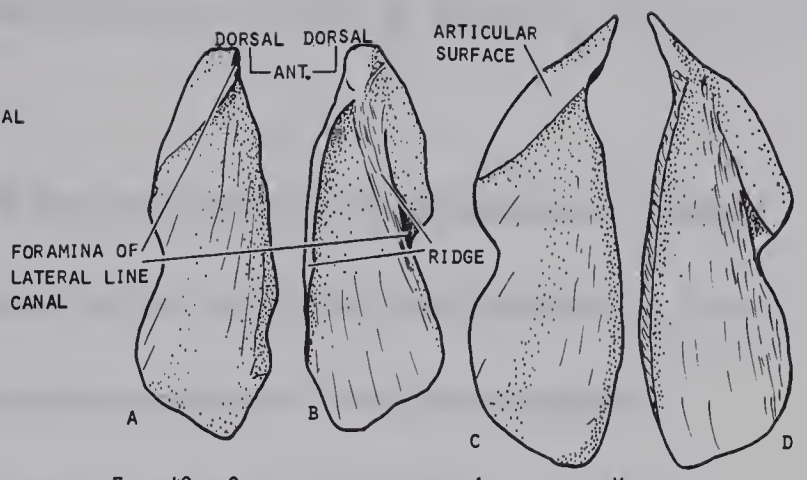


FIG. 40. SUPRACLEITHRA: A, B, AMIA; C, D, KINDLEIA; A, C, EXTERNAL SIDE OF RIGHT; B, D, INTERNAL SIDE OF RIGHT.

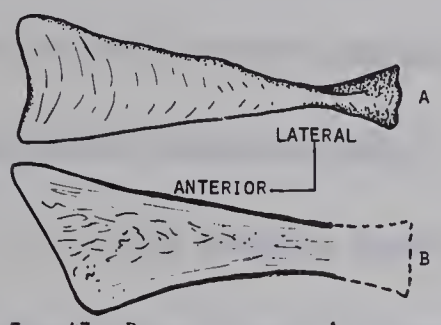


FIG. 43. BASIPTERYGIA: A, AMIA, B, KINDLEIA; A, B, EXTERNAL SIDE.

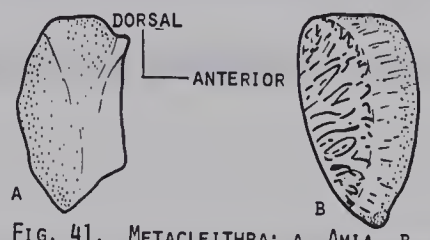


FIG. 41. METACLEITHRA: A, AMIA, B, KINDLEIA. EXTERNAL SIDE OF RIGHT.

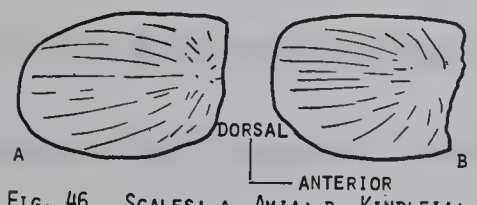
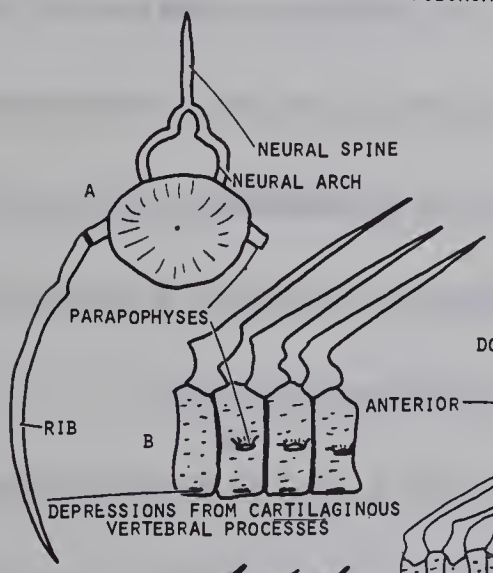


FIG. 46. SCALES: A, AMIA; B, KINDLEIA; A, B, EXTERNAL SIDE OF RIGHT ANTERODORSAL SCALE.

FIG. 42. CLEITHRA: A, B, AMIA (NEARLY IDENTICAL TO KINDLEIA); A, EXTERNAL SIDE OF RIGHT; B, INTERNAL SIDE OF RIGHT.



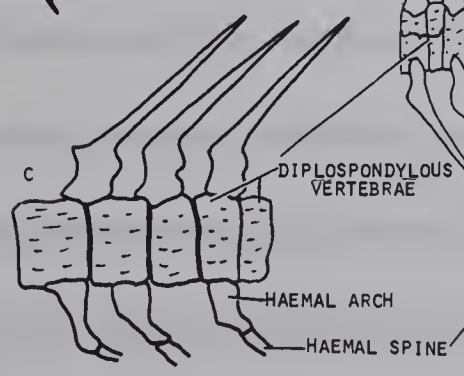


FIG. 44. VERTEBRAE: A, B, C, AMIA OR KINDLEIA; A, ANTERIOR SIDE OF ANTERIOR TRUNK VERTEBRA; B, LATERAL SIDE OF MORE ANTERIOR TRUNK VERTEBRAE; C, LATERAL SIDE OF MORE POSTERIOR TRUNK VERTEBRAE (APPROX. X 1)

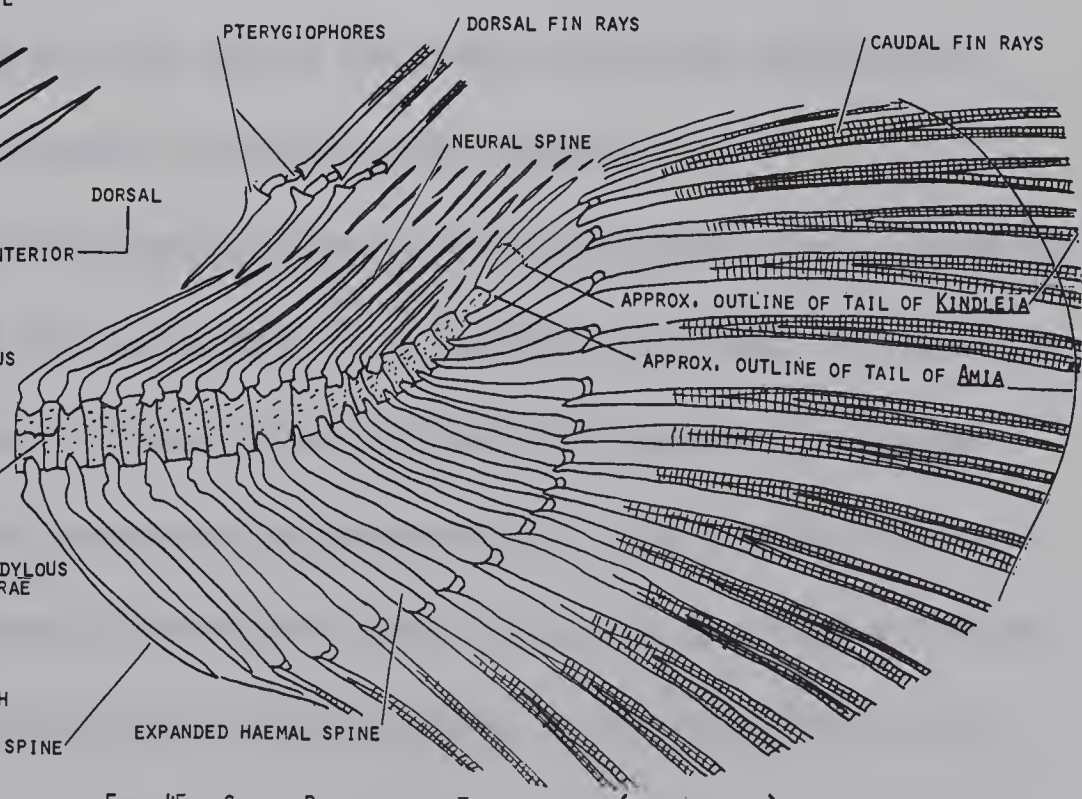


FIG. 45. CAUDAL PEDUNCLE AND TAIL: AMIA (OR KINDLEIA) SIDE VIEW (APPROX. X 1).

NOTE: ALL FIGS. ARE 1.5X UNLESS NOTED OTHERWISE.

Illustrations.-- Fig. 44; Plate III, Fig. 1, Fig. 2; Plate VI, Fig. 1, Fig. 2; Plate VII, Fig. 1.

Description.-- The centra of the vertebrae are amphicoelous, slightly compressed dorsoventrally, and decrease in size anteriorly and posteriorly from the middle part of the column. The anterior surface of the first vertebral centrum is nearly planar at its articulation with the basioccipital. A small notochordal foramen pierces the center of some of the fossilized centra available; others are solid.

The anterior trunk vertebrae support short, paired ventrolateral processes (parapophyses) basal to expanded dorsal ends of posteroventrally inclined, needle-like ribs; both parapophyses and ribs generally increase in size anteriorly. Posterodorsally on each vertebra, and slightly overlapping the anterodorsal surface of the vertebra posterior to it, is a wide neural arch with a long, slender, posterodorsal neural spine arising from it. Ventrally, the ribbed vertebrae bear two shallow depressions on either side of the midline where the cartilaginous vertebral processes that support the dorsal aorta attached.

The vertebrae of the posterior part of the trunk and the caudal vertebrae are somewhat different from the anterior trunk vertebrae; in these, the centra are diplospondylous, with two biconcave discs for each body segment; neural and haemal arches arise from successively alternate centra. The neural arches and spines are not significantly different from those of the anterior vertebrae, but the long, widely based haemal arches that descend from the ventral surfaces of the posterior trunk and caudal vertebrae are restricted to this region. Distally, the more anterior haemal arches bear loosely articulating, long, posteroventrally directed, haemal spines; more posteriorly the spines and arches are fused together.

The haemal spines increase in length toward the caudal peduncle and then decrease in length posteriorly within the peduncle.

Most of the dorsal neural spines and some of the ventral haemal spines extend to, and may insert in the tissue between, the proximal ends of the pterygiophores of the dorsal and anal fins, respectively, but the spines and pterygiophores are not directly connected to each other by bone.

The posterior part of the vertebral column is upturned; the neural and haemal arches and spines in this region are doubled like the central discs, and the haemal spines are expanded in width distally where they support the caudal fin rays. The paired rays separate proximally and articulate with either side of the ventral, distal end of the preceding, expanded haemal spine.

Discussion. -- The parapophyses, neural and haemal arches and spines, ribs and centra of Kindleia resemble closely those of Amia. Significantly different is the fact that in Kindleia the posterior column is slightly more upturned and extends further posteriorly than in Amia; these features suggest that the tail of Kindleia is less abbreviated than that of Amia. Perhaps the more asymmetrical tail of Kindleia produced a greater lifting force in swimming than that of Amia (see discussion of caudal fin, page 75).

According to Lund (1967:204) actinopterygian fishes with abbreviated heterocercal tails possess one centrum in the caudal region supporting two expanded haemal spines; these spines serve for origin of specialized muscles controlling the action of the dorsal lobe of the fin. In Amia, the twinned, expanded haemal spines are usually the seventh and eighth from the ventral-most expanded spine (Goodrich, 1930, fig. 117); similar twinned spines also appear to be present in Kindleia at about the same distance and number of spines from

the ventral one. Lund (1967:198) also mentions that the axial column of fishes is not essential for locomotion, but the evolution of a rigid column enables "the fish to swim with more speed and power". The close likeness of the axial column of Kindleia and Amia suggests that the support it provided and the swimming power it helped produce was comparable in the two genera.

Median Fins

DORSAL FIN

Specimens examined.-- UA 5425, posterior part; UA 5448, posterior part; UA 5497, fragment; other impressions and unnumbered fragments.

Illustrations.-- Fig. 45; Plate VII, Fig. 1.

Description.-- The rays of the dorsal fin are elongate, paired, semicylindrical rods that extend along nearly the entire length of the dorsal midline of the trunk. Proximally, the dorsal fin rays expand into a socket-like structure for articulation with the rounded and thickened distal ends of the long, needle-like pterygiophores. The proximal ends of the pterygiophores, in turn, extend down to insert in the tissue between the upper tips of the neural arches.

Discussion.-- The dorsal fin of Kindleia seems much like that of Amia in its length and form. The pterygiophores in Amia are composed of three bones: a long, inner rod and two, short, rounded, more distal cartilaginous elements. In the sample from the Edmonton Formation the rays and the largest bone in the pterygiophore series are present, and are virtually identical with the corresponding parts of Amia; however, the two smaller distal elements of the pterygiophore seen in Amia are not preserved in the available sample of Kindleia. These elements

were, however, probably present and cartilaginous in Kindleia, as in Amia.

ANAL FIN

Specimens examined. -- An unnumbered impression and possible fragments also unnumbered.

Description. -- The short and narrow anal fin is abdominal on the body, at the midline about midway between the pelvic and caudal fins. The anal fin rays are long and rod-like, expanded proximally and jointed and bifurcated distally. Dorsally, each ray articulates with a long, solid, pterygiophore that, in turn, intervened in the tissue between the distal tips of the haemal spines.

Discussion. -- From the sample collected, the anal fin of Kindleia and Amia are quite similar. In Amia, the pterygiophores that support the anal fin consist of three elements: a long, proximal bone and two, short, distal, cartilaginous elements. The distal segments are not seen in the fossils available, but the articular surfaces for them on the bony segment of the pterygiophore, suggests that, in life, they were present.

CAUDAL FIN

Specimens examined. -- UA 5425, essentially complete; UA 5448, incomplete; UA 5491, nearly complete.

Illustrations. -- Fig. 45; Plate VII, Fig. 1.

Description. -- The abbreviated heterocercal tail is rounded posteriorly, and is nearly symmetrical, but for a slightly greater dorsal length where the dorsal-most rays are longer than the more ventral ones. The long caudal fin rays are paired and semicylindrical, and taper anteriorly and bend ventrally at their

tips; proximally, the pair separate and each articulates with the opposite sides of the ventral, distal end of the expanded haemal spine in front. The proximal parts of each ray are rod-like; parts more distal are segmented and bifurcated.

Disucssion. -- The caudal fin of Kindleia generally resembles that of Amia, but the dorsal caudal rays of Kindleia are slightly longer than those of Amia. According to Harris (1937) and Alexander (1965), a non-symmetrical, abbreviated heterocercal tail provides lift posteriorly with any forward thrust. The slight differences, however, between the rather flexible caudal fins of Kindleia and Amia likely would not be sufficient as to be noticeable in their swimming habits.

Squamation

SCALES

Specimens examined. -- UA 5399, fragment of scaled trunk; UA 5400, fragment of scaled trunk; UA 5409, a scale; UA 5424, a scale; UA 5425, scaled caudal peduncle; UA 5448, scaled posterior part of trunk; UA 5451, fragment of scaled trunk; UA 5454, fragment of scaled trunk; UA 5475, scaled surface of central part of trunk, with numerous lateral line scales; UA 5496, fragment of scaled trunk.

Illustrations. -- Fig. 46; Plate VII, Fig. 1, Fig. 2.

Description. -- In outline, the robust, ovoid to subrhombic scale, slightly longer than wide, is rounded anteriorly and posteriorly; the anterior edge is fairly evenly rounded, but the posterior edge is more rounded ventrally than dorsally. Each scale is overlapped anteriorly by the posterior half of two scales, one more dorsal than the other. Externally, the surface of each scale displays

numerous, fine striations that extend parallel to the dorsal and ventral margins of the scale from a focus located near the center of the anterior margin; the internal surface, except for the slightly thickened dorsal, ventral and posterior edges, bears numerous, minute nodes. The scales of the lateral line system are pierced by a longitudinal canal; the bone surrounding the canal is slightly thickened. The scales increase in size centrally and dorsally, and appear to be in rows that run dorsoposteriorly on the trunk.

Discussion. -- The scales of Kindleia are more highly ossified and more nearly equidimensional than those of Amia, and probably provided a more rigid body covering. The scales vary considerably in size and shape in Amia, but unlike the fossil scales, they are generally more rounded and more nearly symmetrical, thereby producing rows of cyclic rather than rhomboidal scales. The larger scales of Kindleia (as in Amia) occur centrally and dorsally, and the smaller occur anteriorly and posteriorly. The outer surfaces of the scales of Kindleia are striated, as in Amia; the inner nodose surface of the scales in Kindleia contrasts with the smooth, inner surface of the scales in Amia. The annulae or the ganoine layer are not discernible in the fossil specimens.

The trunk of Kindleia, seemingly less flexible than that of Amia, was perhaps restricted slightly in the amplitude of its undulation compared to Amia, although there would most likely be little observable difference in locomotion between the two genera.

Discussion

Summary of Morphology

Kindleia fragosa was an elongate fish with a large head encased in bony plates, a large terminal mouth, a long dorsal fin, an abbreviated heterocercal tail and large, rhomboidal scales.

The dorsal, roofing bones of the broad, deep skull (the extrascapulars, the pterotics, the parietals, the frontals, the dermosphenotics, the nasals, the adnasals and the rostral) are generally well ossified, rigidly associated and strongly ornamented. The roof decreases very little in width from the posterior edge of the extrascapular to the anterior edge of the dermosphenotic, but anterior to this at the excavations for the orbits, the width of the skull roof abruptly decreases. The extrascapulars are symmetrical bones, rounded laterally and tapered medially. The pterotics are notched for the frontals and parietals, and anteriorly, where they meet the posterior edge of the small, tear-shaped dermosphenotics, the bones are constricted into long, narrow lappets. The almost equidimensional parietals meet at the midline along a sinuous suture with the posterior edge of the frontal. The elongate frontals are also paired at the midline, and laterally, the anterior half of the frontal is deeply excavated for the large orbit. Anterior to the frontals, are the small nasals and adnasals; they are, likely, preceded at the tip of the snout by the tiny, medial rostral.

The side of the skull is shielded by the small, oval lacrimal in front of the orbit, two short, thin, suborbitals below the orbit, and two, large dermal postorbitals behind the orbit. The rectangular dorsal postorbital that hugs the edge

of the skull roof and the larger, wedge-shaped ventral postorbital together extend posteriorly almost to the preoperculum.

The arcuate preoperculum that forms the posterior border to the palatoquadrate chamber serves, externally, as the place of attachment for the biting muscles of the lower jaw; the internal surface of the bone bears a distinct ridge for the support and articulation of the anterior edge of the operculum. The opercular series is a broad, bony flap that covers the gill chamber. The large, flat, rectangular dorsal operculum that articulates internally with a process of the hyomandibular and the smaller more ventral subopercular and interopercular gradually decreases in width ventrally.

The underside of the mouth and throat regions of the skull are sheathed with a large, anterior, median gular that attaches at the symphysis of the lower jaw, and a more posterior series of ten, overlapping, blade-like branchiostegal rays. The branchiostegal rays decrease in size ventrally and anteromedially, and each ray articulates anteriorly with the hyoid arch.

The large mouth is rimmed by sharp, conical, lingually curved teeth that are increasingly stout, blunt and peg-like internally. The anterior-most bone of the upper jaw, the triangular premaxilla, extends posteriorly under the nasal, adnasal and the posterior edge of the frontal; it bears a large central foramen for the passage of the olfactory nerve. Posterior and lateral to the premaxilla, the elongate maxilla that is free on all margins except anteriorly where it articulates with the premaxilla, forms most of the upper border to the gape. The upper edge of the posterior half of the maxilla has a deep notch for the biconvex supramaxilla; ventrally, the bone bears a single row of sharp, conical teeth. The external bones of the lower jaw are robust and well ossified, and are deep

dorsoventrally, rounded and thickened dorsally and acute ventrally. The dentary, the largest ossification of the lower jaw, has a single row of sharp, conical teeth on the anterior two-thirds of its dorsal edge. Anteriorly, the two dentaries meet at the wide symphysis; posteriorly, the end of each overlaps part of the angular and the smaller, more dorsal surangular. Two bones fused to the internal surface of the angular of Amia were probably also present in Kindleia; these are the posterodorsal coronomeckelian that articulates with the symplectic and the more central articular that receives a condyle of the quadrate. Internally in the lower jaw, the coronoids and the more posterior prearticular hug the inner side of the dentary and generally bear blunt, peg-like teeth increasing in size medially.

The bones of the palatal complex bear teeth on their internal surfaces. The teeth of the anteromedial vomers, the anterolateral palatines and the anterior part of the more posterolateral ectopterygoid are of two kinds: the outer row consists of sharp, conical teeth; the rest are stout, peg-like teeth that increase in size inward and backward. The remaining bones of the palatal complex (the more medial ectopterygoid, the more posterior and vertical metapterygoid), except the quadrate, bear closely spaced, minute, blunt teeth on their palatal surfaces. The quadrate is firmly attached to the posteroventral margin of the metapterygoid.

Two median, unpaired bones, the parasphenoid and the more posterior basioccipital, form the floor of the braincase. The long, narrow parasphenoid, which has a pair of ascending processes that brace the bone against the small sphenotic above, extends from the vomers to (and completely underlies) the basioccipital. The palatal surface of the parasphenoid bears numerous, minute, blunt teeth. The semicylindrical basioccipital, which articulates with the first

vertebra, has a pair of ventral and lateral foramina for the passage of the intervertebral artery and the sympathetic nerve; it also has one pair of small depressions on the ventral surface, directly behind the foramina, for the ventral, cartilaginous, occipital processes that support the dorsal aorta. Other ossifications of the braincase include a small, triangular opisthotic that underlies the ventral flange of the pterotic and receives the anteroventral process of the suprascapular, and a small sphenotic, located on the ventral side of the posterior part of the dermosphenotic and the anterior tip of the pterotic; the sphenotic receives and supports the ascending process of the parasphenoid.

Ossifications of the hyoid arch consist of a large hyomandibular, a small symplectic and the long, arcuate ceratohyal that probably met at each end with the smaller hypo- and epihyal. The hachet-shaped hyomandibular articulates dorsally with the ventrolateral surface fo the pterotic and the posterolateral surface of the sphenotic, and posteriorly, by a process, with the anterodorsal ridge of the operculum. The bone has a large central foramen for the passage of C. N. VII. The small symplectic, which is posteroventral to the quadrate, bears an articular surface on its anteroventral edge for its hingement with the coronomeckelian of the lower jaw. The ventral edge of the long ceratohyal provides a place of attachment and articulation for the anterior ends of the branchiostegal rays.

The pectoral girdle that supports the small, triangular, ventrolateral pectoral fin consists of a dorsal suprascapular (which underlies the posteroventral part of the extrascapular and which sends an anteroventral process to the opisthotic) a rectangular, dorsolateral supracleithrum, a small, ovoid metacleithrum and a large, ventrolateral L-shaped cleithrum that meets anteriorly at the midline with the other member of the pair. The small, jointed and bifurcated pectoral fin

rays articulate anteriorly with the short pterygiophores that, in turn, probably attached to the cleithrum by cartilage.

Posteriorly, on the outer abdominal part of the body, are the small, fan-shaped pelvic fins, with soft, jointed fin rays that probably articulate anteriorly with four short pterygiophores, which, in turn, move against the distal end of the flattened, dumbbell-shaped basipterygium.

A long, well-ossified, vertebral column, composed of amphicoelous centra, often each with a central chordal foramen, extends from the basioccipital to the tail; the posterior tip of the column is upturned toward (but not into) the rounded, slightly asymmetrical caudal fin. The anterior trunk vertebrae possess ventrolateral parapophyses, long thin ribs and neural arches and spines; the vertebrae of the posterior third of the axial column lack parapophyses and ribs, but have median, ventral haemal arches and spines. In the posterior trunk and caudal regions, the centra are doubled, and the haemal spines of the caudal vertebrae that are also doubled expand distally to support the soft caudal fin rays.

Support for the elongate dorsal fin and the relatively narrow anal fin was provided by bifurcated and segmented, soft fin rays that articulate proximally with the pterygiophores. The proximal ends of the pterygiophores were embedded in the tissue between the tips of the neural or haemal spines.

The robust, well-ossified scales, which increase in size centrally and dorsally over the body, extend in oblique rows over the trunk and caudal peduncle, and provided a thick, rigid covering. Each scale is rectangular to rhomboidal, with rounded edges; the external surface is finely striated and the internal surface bears numerous, rounded nodes.

Parts of the lateral line canal penetrate the roof, cheek, lower jaw and the dorsal bones of the pectoral girdle; the canal extends through the scales along the side of the trunk as well. Beginning anteriorly on the rostral, the lateral line system runs posteriorly through the nasal and the more lateral part of the anterior edge of the frontal. Just behind the posterior rim of the excavation in the frontal for the orbit, the canal curves laterally into the dermosphenotic; here, it branches; one branch enters the dorsal postorbital, and the other branch enters the pterotic. The ventral branch continues along the anterior edge of the dorsal postorbital into the ventral postorbital (with a secondary, longitudinal canal within the ventral postorbital), and then curves anteriorly into the suborbitals, lacrimal, the adnasal and back to the rostral. The posterior branch extends backward along the lateral edge of the pterotic, extrascapular and suprascapular, and then it veers ventrally into the supracleithrum; from the middle of the posterior border of the supracleithrum, the lateral line continues along the side of the trunk. In addition, two canals run transversely across the skull roof and connect on either side with the anteroposterior canal; one extends along the posterior third of the pterotic and parietal (with a secondary offshoot within the parietal directed to the anterolateral corner), and the other passes through the length of the extrascapulars. A lateral line canal also extends ventrally from the posterior part of the pterotic, through the preoperculum and anteriorly through the ventral part of the lower jaw, with a small branch that travels along the posterior edge of the angular.

Intraspecific Variation

Most of the changes in the cranial and postcranial bones during growth involve an increase in the size and in the degree of ossification of the bone.

UA 5450, UA 5456, UA 5421 and UA 5398 respectively, exhibit a progressive increase in the size of each bone. The younger (smaller) individuals have a greater excavation in the frontal for the orbit in relation to the width of the roof. The relative ratio of the length of the frontal to the length of the parietal increases from approximately two and one-half times in the smaller to three times in the larger specimens. The surface ornamentation of the external bones of the skull becomes more distinct and the grooves and ridges become more widely spaced with an increase in the size of the bone. An increase in the size of the preoperculum sees more strongly ornamented ventrolateral and posterolateral borders. In UA 5484, UA 5505, UA 5506 and UA 5507 the width of the symphysis of the lower jaw remains relatively constant; an increase in the size of the dentary shows mostly in its length and in its posterior width. Increase of size of the tooth-bearing bones and the teeth appear to be co-ordinated. Most of the lateral line system is as well developed in the smaller as in the larger specimens with the only obvious exception being that the surface groove of the longitudinal canal of the ventral postorbital is deeper in larger specimens.

If one neglects the differences in sizes of individuals, then the amount of variation in characteristics within the different specimens is remarkably slight. The number of teeth on the dentary and maxilla is reasonably stable (about 15 and 25, respectively) but the number of teeth on the palatal and coronoid ossifications is more variable (vomers, 16-25 teeth; dermopalatines, 20-25 teeth; coronoids, 8-14 teeth). The inner teeth are not aligned in discrete rows, nor are they placed in the same position in all specimens; rather, they occur somewhat scattered over the toothed surface of the bone.

Minor degree of variability exists in the angularity or the amount of curvature of certain bones. The ventral apex of the interoperculum can be rounded or truncated; the extrascapular can be abruptly or evenly tapered, medially. A pertinent generalization is that the morphology of Kindleia seems extremely stable, apparently even more so than that of Amia.

The preservation of meristic components was too poor and their numbers too few to make any conclusions about changes in meristic characters within the population. The limited amount of variability seen, however, in the dentition of the sample collected suggests that repetitive features were probably nearly as stable as the non-meristic characters.

Comparisons

Estes (1964:37) included in the Family Amiidae the following genera: Sinamia Stensio, Paramiatus Romer and Fryxell, Pseudamia Lehman, Urocles Saint-Seine, Amiopsis Woodward, Protamia Leidy (= Pappichthys, Cope, 1873), Kindleia Jordan (= Stylomyleodon, Russell, 1928a) and Amia Linné (= Notaeus and Cyclurus, Agassiz, 1843). The discussion in this section will be divided into two parts: (1) an extensive comparison of Kindleia and Amia and (2) a part contrasting Kindleia with other amiids.

Kindleia and Amia

The fossil amiid, Kindleia fragosa, is very similar in many features to the modern species, Amia calva, although significant differences are also evident. Figure 47 includes diagrammatic reconstructions of Kindleia and Amia that

attempt to summarize and to distinguish the features of the two genera.

Both Kindleia and Amia are elongate with large heads and mouths, long dorsal fins and abbreviated heterocercal tails.

The cranial bones, especially the endochondral ones, are better ossified in Kindleia than in Amia; invasion of much secondary cartilage has occurred in Amia. The skull roof is less flared laterally and more rounded posteriorly, and the notches in the pterotic for the frontal and the parietal, the excavations in the left parietal for the right and the excavations in the frontal for the orbits are more extensive in Kindleia than in Amia. The ratio of the length of the external surface of the frontal to that of the parietal is greater in Kindleia; this is the result of a less variable frontal-parietal suture. Because of the excavation in the pterotic for the frontal, the anterior lappet of the pterotic and the posterior edge of the dermosphenotic are narrower in the extinct genus. There is no indication that Kindleia possessed supraorbitals as Estes (1964) suspected; in fact, the regularity and smoothness of the edge of the frontal dorsal to the orbit suggests that this part of the bone formed the dorsal rim to the orbit. The posterior part of the lacrimal and the whole of the anterior suborbital are slightly narrower than those of Amia. The dorsal and ventral postorbitals of Kindleia cover a greater part of the cheek region and form a wider posterior rim to the orbit. The rectangular dorsal postorbital is wider anteriorly than the more triangular, modern counterpart, and the wedge-shaped ventral postorbital is the larger of the two postorbitals in Kindleia, but the reverse is true in Amia.

The preoperculum, subopercular and interoperculum are almost identical in the two genera, but the operculum is more equidimensional and more rounded anterodorsally, and the posterior edge is more nearly vertical in Kindleia than in

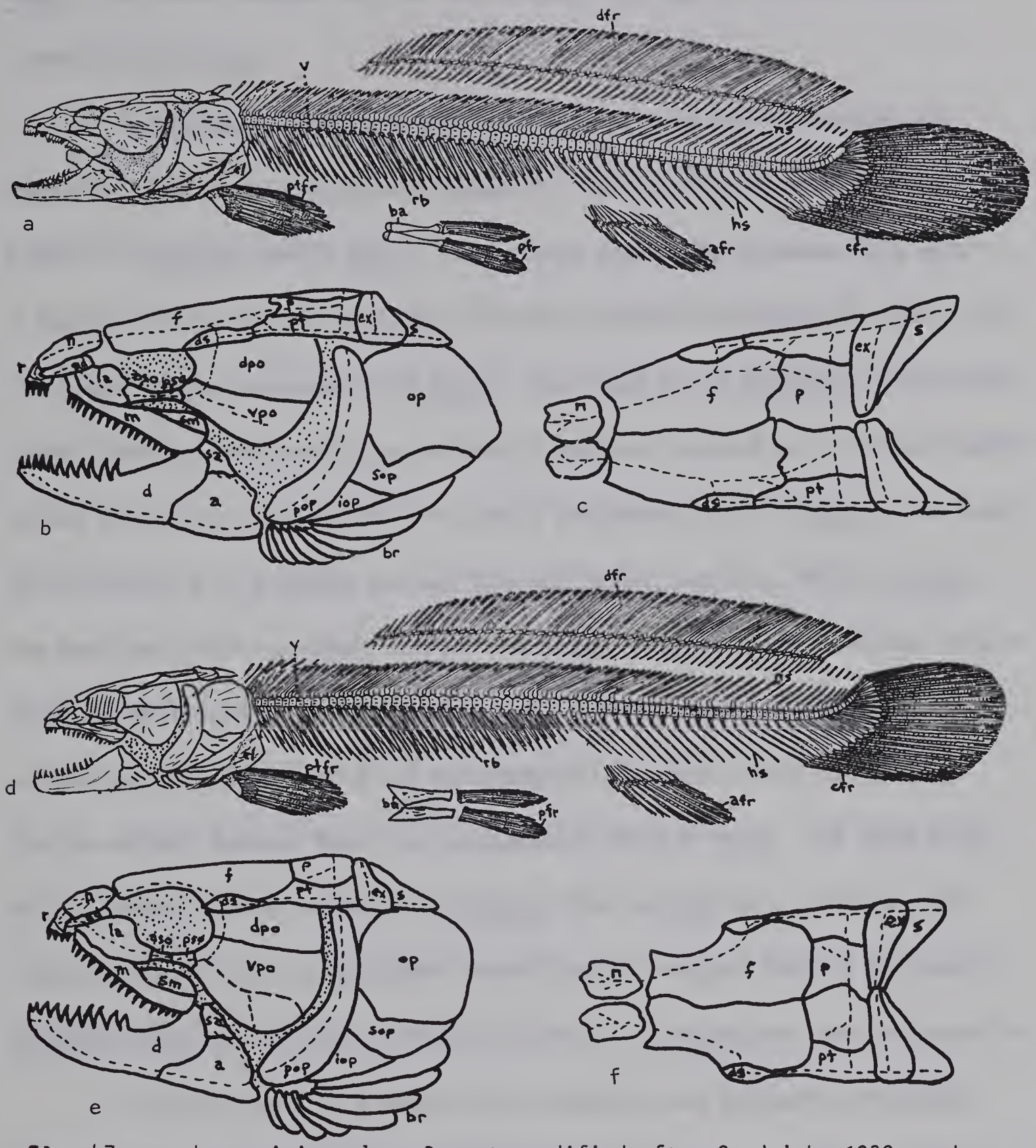


Fig. 47. a, b, c, Amia calva, Recent, modified after Goodrich, 1930, and Estes, 1964; a, skeleton; b, side view of skull; c, dorsal view of skull: d, e, f, Kindleia fragosa, restored; d, skeleton; e, side view of skull; f, dorsal view of skull: dashed lines indicate lateral line canal system. Abbreviations: a, angular; ad, adnasal; afr, anal fin ray; aso, anterior suborbital; ba, basipterygium; br, branchiostegal rays; cfr, caudal fin ray; cl, cleithrum; d, dentary; dfr, dorsal fin ray; dpo, dorsal postorbital; ds, dermosphenotic; ex, extrascapular; f, frontal; hs, haemal spine; iop, interoperculum; la, lacrimal; m, maxilla; n, nasal; ns, neural spine; op, operculum; p, parietal; pfr, pelvic fin ray; pop, preoperculum; pso, posterior suborbital; pt, pterotic; ptfr, pectoral fin ray; r, rostral; rb, rib; s, suprascapular; sa, surangular; sm, supramaxilla; sop, suboperculum; v, vertebra; vpo, ventral postorbital.

Amia. The branchiostegal rays are more robust, less tapered distally and less numerous in Kindleia.

The bones of both upper and lower jaws and the palatal complex are generally alike in the two genera, except for the more lingual teeth that are blunter in Kindleia than in Amia. The anterior part of the supramaxillary notch is deeper in the maxilla of Kindleia and holds a biconvex supramaxilla rather than the wedge-shaped supramaxilla of Amia. The lower jaw of Kindleia is more robust, deeper anteriorly and more acute ventrally, and the coronoids are wider and extend farther downward, hugging the inner side of the dentary, than in Amia. The teeth on the coronoids of Kindleia are peg-like and largest medially, while in Amia the teeth are sharply pointed, conical and largest laterally. The numerous, minute teeth distributed on the internal surfaces of the prearticular, parasphenoid, ectopterygoid, entopterygoid and metapterygoid resemble in size and position (but are slightly blunter than) the corresponding teeth of Amia. The teeth of the palatal bones are more numerous in Kindleia than in Amia and, except for the external row of sharp, conical teeth resembling the marginal teeth of the gape of Kindleia and all of the teeth of Amia, the teeth of Kindleia are stout and peg-like.

The parasphenoid, basioccipital, opisthotic and sphenotic are slightly more ossified in Kindleia; the parasphenoid is thicker dorsoventrally, and shows a higher, median dorsal ridge, thicker ascending processes and more squared posterior flanges than in Amia. In Amia, the addition by fusion of a vertebra to the back of the basicranium produces a second pair of ventral depressions and increases the length of the basioccipital so that the parasphenoid no longer underlies it in its total length.

Ossifications of the hyoid arch and the pectoral girdle are closely alike in Kindleia and Amia. The supracleithrum tapers dorsally to a point rather than being squared as in Amia. The ovoid metacleithrum of Kindleia is unlike the bean-shaped bone of Amia, and the cleithrum of Kindleia is wider and more heavily sculptured than the modern counterpart.

The remaining postcranial structure is remarkably alike in the two genera. Except for a slight difference in the degree of ossification, the pterygiophores and the rays of the fins are similar in Kindleia and Amia. However, the basipterygium is broader and flatter, the upturned vertebral column extends farther posteriorly, and the scales are thicker, broader and less rounded posteriorly in Kindleia than in Amia.

The lateral line system of Kindleia conforms closely with that of Amia, except for the longitudinal canal of the ventral postorbital, which is longer and more distinct in Kindleia, and the additional interconnected system of the frontal, pterotic and parietal of Amia. The latter extends from the center of the frontal to the posterior edge of that bone, where it branches; one line enters the parietal and connects with the transverse canal of that bone, and the other branch enters the pterotic and connects with its longitudinal canal.

Kindleia and Other Amiids

Janot (1967) synonymized Kindleia and Amia, but in view of the preceding discussion comparing Kindleia and Amia, especially considering the specializations in Kindleia for a more durophagous diet, a generic separation is justified. (Refer to a more detailed discussion of Janot's paper on page 101 of this manuscript).

In 1935, Stensio described most of the skeleton and reconstructed the skull of Sinamia zdanskyi, from the Lower Cretaceous of China. The rhombic scales and the occurrence of ganoine on the exoskeleton and some of the dermal bones of the head of Sinamia are primitive features not seen in Kindleia. The eight to ten (sometimes partly fused) extrascapulars and the single large median parietal probably represent specializations peculiar, among the amiids, to Sinamia. Other features are of uncertain significance, and may be either primitive or advanced; these are: the presence of supraorbitals, a low otic process on the metapterygoid, a narrow hyomandibular that lacks a central foramen for the hyoideo-mandibularis branch of C.N. VII, a gular tapering to a point anteriorly, short postorbitals, and a short dorsal fin. Estes (1964:39) doubted that the metapterygoid is primitive, but it, along with the absence of a foramen on the hyomandibular, may simply be generically variable within the Family Amiidae. Sinamia resembles Kindleia in the broader posterior part of the parasphenoid, the notches in the pterotic for the parietal and the excavations for the orbits; it is much like Amia in the shape of the operculum, the number and shape of the branchiostegal rays and in the shape of the lower jaw and teeth.

Urocles (Saint-Seine, 1949, fig. 76b), known from Jurassic deposits of Europe, like Kindleia has enlarged lower postorbitals, prominently excavated frontals and no supraorbitals. In Urocles, however, the lacrimal is fused to the anterior suborbital, and the ventral postorbital is fused to the posterior suborbital; perhaps this rigidity in the cheek is a primitive condition, with a trend to increased flexibility of the cheek in later amiids.

The Late Jurassic and Early Cretaceous Amiopsis of Belgium and England

(Woodward, 1919:90) is closely similar to Kindleia, but Amiopsis has four smooth supraorbital plates and a short dorsal fin on the middle of the trunk.

Lehman (1951) described Pseudamia heintzi from Eocene sediments in Spitzbergen. The species is nearly identical to Amia calva and Kindleia but for the Sinamia-like metapterygoid that lacks a prominent otic process, a concave notch on the posterodorsal border of the operculum and short postorbitals (as restored by Lehman, fig. 1). Estes (1964:39) noted that the concavity of the operculum can also occur in Amia and that Lehman's postorbitals were actually too broken "to warrant restoration". The metapterygoid of Pseudamia and possibly that of Sinamia may be primitive in form, or it may be a variable feature that has recurred in at least one genus of amiid later than Sinamia.

Paramiatus gurleyi Romer and Fryxell (1928) from the Eocene Green River Formation of Wyoming is a short, deep bodied amiid. The restored skull (ibid, fig. 3) appears to be like that of Amia but for its short postorbitals and opercula, both of which are wider than long. The subopercular and surangular shown in the restoration retain the original displacement but were actually probably more like those of Kindleia and Amia. Paramiatus differs from Kindleia in its depth and shortness of the body and bones of the skull, in its lack of an excavation in the frontal for the orbit, and in its lack of a notch in the pterotoic for the parietal and the frontal; the dorsal fin (ibid, fig. 1) is slightly shorter beginning farther posteriorly, and the caudal fin is more symmetrical than in Kindleia. The ossification labelled ptf (postfrontal) by Romer and Fryxell is synonymous with the dermosphenotic of this paper; another bone obviously printed wrongly as pf (preopercular) and probably meant to read pf (prefrontal) might be a supraorbital

as Estes (1964:39) suggested, or more possibly, it is a sphenotic (although I cannot be certain without seeing the original specimens).

Protamia, first described by Leidy (1873:78) and reported subsequently from Upper Cretaceous and Paleocene sediments of Saskatchewan, Alberta and Montana, and also from the Eocene of Mongolia (see Estes, 1964:41 and 42) is a large amiid similar in form to Amia. Most references to Protamia include descriptions of vertebrae; these are nearly identical in shape to, but are much larger (approximately three times) than those of Amia calva. Hussakof (1932:8 and figs. 7-24) identified and refigured cranial material of Protamia, which Estes tentatively assigned to Amia; Hussakof's specimens closely resemble those of Amia but are distinctly larger, and are somewhat suggestive of the difference in size seen in the vertebrae of these two genera.

Many species of Amia have been described but most differ very little from Amia calva (see Romer and Fryxell, 1928:523; Dechaseaux, 1937:13; Janot, 1967:143). In 1964 Estes (p. 40) redesignated the species Amia munieri (Priem, 1911) of the Oligocene of France (refigured and described by Dechaseaux, 1937) as Kindleia munieri based on the following characters of K. munieri that are essentially like those of K. fragosa: the frontals are about three times the length of the parietals; the large ventral postorbital, the wider of the two postorbitals, bears a prominent longitudinal lateral line canal; the marginal teeth are sharp and conical, and the palatal teeth are blunt and peg-like; the operculum is nearly quadrate, and the branchiostegal rays are rounded (see Priem, 1911, fig. 40; Dechaseaux, 1937, figs. 2, 5 and Estes, 1964, fig. 19). K. munieri differs from K. fragosa in the lack of a wide excavation in the frontal for the orbit, but, as Estes (1964:40) commented, a decrease in the size of the orbit might have

developed in parallel in the evolution of Kindleia munieri and Amia calva.

Paleontological Interpretation

Kindleia fragosa has many osteological characteristics that are similar to those of Amia calva, other traits that are more primitive than those of the Recent genus, and yet other features that represent specializations for its particular niche.

The skeleton of Kindleia is relatively well-ossified, robust and fairly rigid. The presence of notches in the pterotics and parietals, the wide unornamented flanges of many cranial bones that underlie and form a suture with an adjoining bone and the thick, rigid branchiostegal rays indicate that the bones of the skull of Kindleia were tightly bound, with only limited capacity for movement or flexion. In comparison, the degree in, or absence of, ossification, notches, and wide areas of overlap, along with the possible appearance of new centers of articulation (for example, the prominent indentation on the internal surface of the extrascapular), in Amia, suggest a greater flexibility within the cranium. An increase in the amount of cartilage in Amia is probably the result of a trend in evolution from the ancestral, more nearly Kindleia-like, heavier and thicker skeleton to a lighter structure that allows for greater maneuverability but still assures considerable support. Similar trends are seen in the evolution from holosteans to teleosteans where a decrease in the thickness of the bone lessens the weight, while the development of cross-supports within the bone maintains its strength.

The skull of Kindleia is short and deep with a length just slightly greater

than one and one-half times the depth (in comparison to a length in Amia of about two times the depth). The rounded posterolateral edge of the skull roof, the squared operculum, the deep anterior part of the dentary and possibly the biconvex supramaxilla give the skull of Kindleia a less tapered and less streamlined appearance than that of Amia. Much of the increase in the length of the skull of Amia is related mainly to the fusion of a vertebra to the basioccipital, although this is accompanied by an effective increase in the length of some of the more external bones of the skull: the extrascapular and suprascapular are more angular and more flared posterolaterally so that together they are longer at the roof edge, the operculum is longer, and the branchiostegal rays are more numerous in Amia than in Kindleia. The addition to the basioccipital increases the length from the point of pivot to the anterior tip of the jaw, thereby effectively increasing the possible arc of rotation at the anterior part of the skull. According to Gray (1933), modern fishes generally turn by flexures of the head, not the tail; so perhaps the seemingly greater mobility of the skull of Amia allows for greater ease of turning than the skull of Kindleia. The more bulky skull of Kindleia may, in part, be a retention of ancestral proportions, but also the thickness and strength of the bone could be a result of the acquisition of a more rigid skull to support a crushing jaw mechanism.

Large postorbitals over the cheek region restrict the size of the adductor mandibularis muscle; a decrease in size of these bones permits a potential increase in the power of adduction of the lower jaw (Schaeffer and Rosen, 1961). The latter is seen commonly in actinopterygian evolution (Schaeffer and Rosen, 1961; Gardiner, 1967) and could also explain more limited differences within the

Family Amiidae, for example, those differences between the larger postorbitals of Kindleia and the smaller postorbitals of Amia.

The tight association of branchiostegal rays in Kindleia produces a relatively stiff flap that covers the underside of the throat region. Contraction of the hyohyoideus muscle pulls the ventral surface of the oral cavity upward and thereby helps in forcing water through the gills and out the opercular slit; relaxation of the muscle allows water to enter the cavity. A more flexible branchiostegal series could increase the "pumping" effect of the ventral flap. In actinopterygian evolution, there is a trend toward a decrease in numbers, width and rigidity of the branchiostegal rays, with a corresponding increase in flexibility. The more robust and probably less pliant branchiostegal rays of Kindleia are likely more primitive; those in Amia probably departed from the ancestral condition during the evolution of the central predaceous line. Other seemingly primitive features of the respiratory mechanism of Kindleia might be correlated with that discussed above. As noted previously in this text, the association of the point of pivot to the place of muscular insertion on the operculum suggests that the gill slit of Kindleia was not as expandable as in Amia, but with the increased pumping effect of the branchiostegal series of Amia, a wider gill aperture for excurrent flow was an advantage.

The series of dense overlapping scales of Kindleia (also probably a primitive character) produced a relatively stiffer and heavier body covering in Kindleia than in Amia that might have had a slight effect on the amplitude of body undulations and in the amount of drag during locomotion. The early

development of diplospondyly in the caudal region of amiids resulted in some increase in flexibility of the vertebral column. Such flexibility is useful in slow undulatory motion, but it does not allow for the production of as great power or speed from movement of the caudal fin.

The differences between the scales and fins of Kindleia and Amia, however, are seemingly not significant enought to make any sufficient distinction in the pattern of locomotion between the two genera. The swimming habits of Kindleia were probably quite similar to those of Amia, that is, mainly slow, steady movement by undulations of the long dorsal fin and to some extent from the caudal fin, with lift and some maneuvering accomplished by the paired fins. The wide pectoral fins (and possibly the slightly depressed head) act partly as planes that lift the fish and compensate for any downward force imparted by the asymmetical tail and the weight of the dermal bone (Harris, 1936; Alexandar, 1965); these fins and the pelvic fins affect pitching, and, as well, in most Holostei and Teleostei, the paired fins are capable of undulatory motion for hovering (Harris, 1938). Kindleia has a slightly less abbreviated heterocercal tail and a heavier skeleton than Amia; therefore, the presence of a more ossified and slightly wider pectoral girdle in Kindleia perhaps provided for greater lift. The pelvic fins may also help to retard rolling (Lagler et al., 1962:193), although Harris (1938:43) refuted this idea and maintained that the dorsal and anal fins are the "main

anti-rolling devices". In Kindleia, the pelvic fin seems to be slightly larger and is supported internally by a broader basipterygium than in the extant genus, but the narrower-based pelvic fin of Amia, although less powerful, is probably more flexible. If the pelvic fins do have some effect in the stability of the fish, then it was probably more pronounced in Kindleia than in Amia. However, with the increase in symmetry of the tail and a decrease in the weight of the dermal bone of Amia, the pelvic fins, as well as the pectorals, possibly could be used more for maneuvering than for providing stability.

The specializations of Kindleia reflect a more durophagous diet than that of Amia. The deep, lower jaw with a wider symphysis and the thick, palatal and wide coronoid ossifications, the rigidity within the skull and the large number of internal, peg-like teeth are acquisitions that would enhance the function of a crushing jaw mechanism. The sharp, conical, marginal teeth retained from the ancestral predaceous stock are suited for seizing of food, but the lingual teeth are multiplied and modified and better suited for breaking and crushing.

The seemingly large orbits of Kindleia (as evidenced by the larger excavations in the frontals and the wider anterior edge of the postorbitals) and the possibly larger olfactory foramen of the premaxilla suggest that the fossil genus might have relied on sight and olfaction to a greater extent than Amia. The large excavations in the frontals for the orbits are present in the earliest known amiid, Urocles from the Jurassic of Europe, and also in other fossil amiids, and could well be an ancestral character that has been modified, in parallel, in Amia and Kindleia ("Amia") munieri (Dechaseaux, 1937). The significance of the deeper and longer groove produced by the lateral line canal

of the ventral postorbital of Kindleia is unknown, but it is seemingly related to the decrease in the size of the bone in Amia, and possibly the change of the lateral line canal to a more superficial position in Amia than in Kindleia. In the lateral line system of the dorsal roof of the skull, the short terminal branches of Kindleia are seen to be lengthened and interconnected in Amia and these possibly represent a more advanced stage in the evolution of the lateral line sense among the amiids.

Kindleia fragosa is closely alied to Kindleia munieri: the two species are amiids that have a specialized crushing dentition. The Jurassic genus, Urocles, and the Lower Cretaceous genus, Sinamia, are likely not far removed from the ancestral amiid stock that gave rise to the rest of the members of the family. Urocles has enlarged postorbitals and excavated frontals, as in Kindleia, and is probably nearer to the generalized ancestor than the slightly more specialized genus, Sinamia. The Family Amiidae that arose directly from the Family Caturidae: Amiiformes (Gardiner, 1967:204), therefore, might consist of two major groups that split from a common ancestor before the Late Jurassic. One such group tentatively includes the specialized Sinamia and probably Amiopsis and Pseudamia, and is characterized by members that possess metapterygoids with a low otic process, supraorbitals, short postorbitals and a relatively short dorsal fin. The second, more generalized group, which has genera with long otic processes, no supraorbitals and long postorbitals, includes the earliest known amiid, Urocles. Likely, from a Urocles-like ancestor, after the establishment of a trend to lengthening of the dorsal fin and an increase in the flexibility of the cheek, there were two offshoots from the central stem that lead to Amia; one of these offshoots gave rise to Protamia and the other to Kindleia. Both the central, generalized line and the specialized

Kindleia-like line probably developed smaller orbits in parallel. The above discussion of phylogeny of the amiids includes all presently known genera but Paramiatus, which, from present knowledge, can be placed with either of the two main groups.

The phyletic chart (Fig. 48), is an attempt to summarize the various features that separate or unite the lineages of amiids. The chart, however, is only tentative ; the paleontological evidence of most of the amiids and certainly the studies of fresh water Mesozoic and Cenozoic deposits is so limited as to make the establishment of any conclusive relationships impossible. I do not intend to speculate on or to defend the geographic discrepancy between Kindleia fragosa, known only from North American deposits, and Kindleia munieri, known only from European sediments. It certainly is plausible to invoke fresh water connections between the Western and Eastern Hemispheres (either by supporting pre-Mesozoic union of the continents or by land bridges of the Bering Strait during various times of the Tertiary or Pleistocene), but, at present, firm information is too scarce, thereby making such conjecture fruitless. The relationships discussed here are based solely on morphological similarity, although the possibility of resemblance owing to parallelism cannot be refuted. I agree with Mayr, Linsley and Usinger (1953:46) that the delimitation of significant characters (characters on which relationships or distinctness are made) is somewhat subjective. The determination of what constitutes a derived or specialized character is a difficult but useful step in trying to construct a true phyletic diagram.

According to Mayr, Linsley and Usinger (1953:49) a genus can be considered as a group of species adapted to a particular mode of life, the mode usually expressed in morphology. The development of specializations for a particular mode

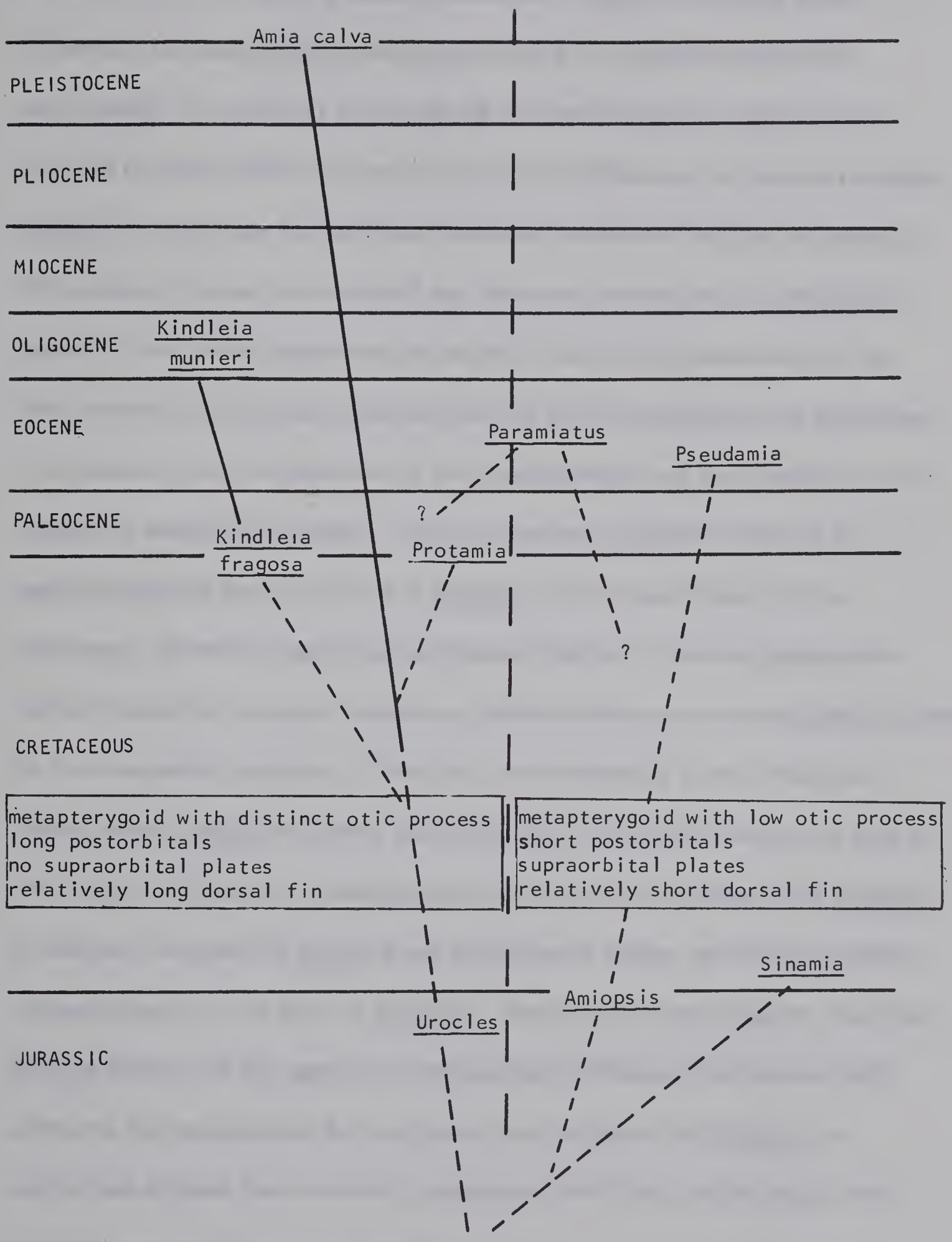


Fig. 48. Hypothetical phyletic chart of the Family Amiidae.

of life, therefore, may be a generic character. Applying this point to the differences between Kindleia and Amia (keeping in mind other features of relationship), it is difficult to include the two genera under a single genus as proposed by Janot (1967); she maintains that the differences in characters between Kindleia and Amia are not sufficient to warrant a separate designation for each. Her synonomy is based on the belief that the primitive features of Kindleia (the frontal is three times longer than the parietal; the frontal is excavated for the orbit; the dorsal postorbital is smaller than the ventral postorbital; the operculum is rectangular, and the distal end of the branchiostegal rays are rounded) are too variable to establish two genera. Janot, however, neglects to mention the specializations of dentition found in Kindleia. As has been shown in this manuscript, the above features are sufficiently distinct in the two genera to be used as a basis for taxonomic separation; the distinctions cannot simply be accounted for by intraspecific variation. Certainly, as mentioned by Estes (1964), the palatal teeth of Amia are blunter and shorter than the marginal teeth, but they are still conical with narrow, rounded apices and are not flat-crowned as in Kindleia. In addition, the teeth of Amia are not multiplied in number nor do they increase in size lingually as the teeth of Kindleia. Dental morphology suggests, therefore, that the diets of the two genera are predominantly different; this feature itself advocates the separation of the two genera, and suggests that Kindleia is a specialized offshoot from a central, predaceous amiid line, while Amia is the surviving member of the central stock.

Only four genera of amiids have been reported to date from North America, namely, Kindleia from the Upper Cretaceous and Paleocene, Paramiatus from the

Eocene of Wyoming (Romer and Fryxell, 1928), Protamia (= Pappichthys) from the Upper Cretaceous to Eocene (Leidy, 1873:78; Cope, 1873; Russell, 1928a; Brown, 1907; Gilmore, 1924) and the Recent genus, Amia; this assemblage is probably composed of three side branches from a central stock (Fig. 48). Kindleia is specialized for at least a partial diet of hard-shelled invertebrates; Paramiatus is a shorter, deep, perch-like form; Protamia is a "giant", Amia-like fish, and Amia is a relatively generalized predaceous fish. It is apparent (from present knowledge) that during the Late Cretaceous and early Tertiary at least three amiids were inhabiting the rivers and streams of North America. Two of these genera show closely related remains from the Eastern Hemisphere; a fish very similar to Kindleia fragosa, Kindleia munieri (= Amia munieri, Dechaseaux, 1937), is known from the Oligocene of France, and Protamia is also known from the Eocene of Mongolia (Hussakof, 1932:7). The Late Jurassic and Early Cretaceous genus, Amiopsis, and the Eocene genus, Pseudamia, are known only from European localities and are rather generalized amiids not far removed from the central stem, although they are tentatively associated with the Sinamia-line of evolution because of their short otic process, their short postorbitals and their supraorbitals. The older and near-basal amiids, Urocles (Saint-Seine, 1949, fig. 76b) of the Upper Jurassic of Europe and Sinamia (Stensio, 1935) from the Lower Cretaceous of China, indicate the early, relatively wide geographic distribution of the family.

The existence of a central predaceous form which may have given rise to the more specialized groups and to Amia, has not yet been discovered in North America. There is a strong suggestion that with the presence of more primitive and earlier more generalized amiids than Amia in the Eastern Hemisphere and the

occurrence of similar taxa on the two continents that, at some time prior to the evolution of Amia calva, generalized predaceous amiids existed in North America. The possibility remains, of course, that the modified genera originated in a particular area and radiated outward, or that the existence of similar forms on the two hemispheres represented parallel evolution from a widely distributed basal stock; either case, however, suggests the existence of an ancestor to Amia in North America sometime prior to the latest Tertiary, and either situation also supports the generic separation of Kindleia and Amia.

PALEOECOLOGICAL INTERPRETATION

Following extensive transgression and deposition of the marine Bearpaw Formation in late Campanian time, tectonic activity in the Cordillera forced the withdrawal of the sea southeastward. The sediments of the lower part of the upper Edmonton Formation (Late Maestrichtian) represent deposition in fluvial or flood plain conditions in a warm - temperate environment (Srivastava, 1968). The well-sorted sediment and the low content of clay indicates transport in relatively clear rivers and streams, with moderate to slow currents, typical of coastal plain conditions.

The floral assemblages (Bell, 1949 and 1965, and Srivastava, 1968) include a large number of water plants that suggest the presence of marshy areas, in addition to coniferous trees indicative of forested areas.

Invertebrates, especially non-marine molluscs, are known from the lower Edmonton but not from the upper Edmonton Formation (Tozer, 1965:16); this may indicate that much of the studied parts of the upper Edmonton Formation represent sediments that were deposited in sidestreams and not in the larger rivers or tributaries in which molluscs seem to be most abundant (Estes, 1964:164).

The known lower vertebrate fauna of the upper part of the Edmonton Formation (Langston, 1965) is extremely limited, especially when compared to the taxonomic abundance of small mammals (Lillegraven, 1969): this discrepancy may represent a bias of preservation or collection; only a detailed study of the smaller lower vertebrates will clarify this dilemma. The four fish reported to date from the upper Edmonton Formation (Myledaphis, Acipenser, Lepisosteus, Kindleia, Langston, 1965) are also found in the Lance Formation and according to Estes

(1964:160-161) are inhabitants of sandy bottomed rivers near the coast.

The unusual occurrence of numerous specimens of Kindleia that range in size from juvenile to adult in a rather restricted bed void of other macrofossils, may indicate slightly abnormal conditions of death and burial. Perhaps the fish became trapped in a pond or tributary that was separated from the main channel. The presence of considerable carbonate cement in the sandstone may be the result of precipitation upon evaporation and concentration.

The habitat of Kindleia was probably not unlike that of modern Amia; the animal was probably a dweller in slow-moving rivers and tributaries that empty into the sea. If Kindleia did retreat to smaller tributaries, possibly to escape the predaceous fish (Lepisosteus) or to avoid competition with the other mollusc and arthropod consumers (Myledaphus and Acipenser) which today prefer larger rivers, then there would be a greater possibility of separation and isolation from more permanent bodies of water. Death might result from concentration of salts rather than complete desiccation; such a locality might provide a favorable environment for preservation and burial.

The sediments, the flora and the known parts of the fauna of the Upper Edmonton Formation are similar to those of the Lance Formation. The sandstones are relatively silt-free and the flora in both instances is indicative of closely approximated swampy and forested areas. Kindleia, therefore, probably inhabited fresh water streams and tributaries that enter into the sea over much of the western interior of North America in the Late Cretaceous.

SUMMARY

Well-preserved and articulated specimens of Kindleia fragosa from the upper part of the Edmonton Formation (Maestrichtian) of Alberta permitted a detailed study and restoration of the skeleton.

Kindleia fragosa, which is similar to the modern Amia calva of eastern North America, has a large head, covered by bony plates, a large terminal mouth, postorbitals that cover the cheek, a single median gular, a series of broad branchiostegal rays, a long dorsal fin, an abbreviated heterocercal tail, small abdominal pectoral and pelvic fins and thick overlapping scales. Kindleia differs from the extant genus in the possession of: (1) a greater degree of ossification of the skeleton, (2) a large orbit, (3) a longer frontal in relation to the length of the parietal, (4) prominent notches in the pterotic for the parietal and frontal, (5) a biconvex supramaxilla, (6) a larger ventral than dorsal postorbital, (7) a wider lower jaw, (8) numerous peg-shaped interior teeth, (9) more robust and less tapered branchiostegal rays, (10) a nearly square operculum, (11) a more extensive, upturned axial column, and (12) wider pectoral and pelvic girdle bones.

The degree of ossification, the large mouth, the short skull, the single median gular, the numerous broad branchiostegal rays, an abbreviated heterocercal tail, heavy sub-rhombic scales, large cheek bones and, possibly the size of the orbit, are ancestral characters retained in Kindleia, but which were altered to some extent in the evolution of Amia calva.

The existence of numerous, peg-shaped teeth and the increase in the strength of the skull are specializations for a durophagous diet (probably a diet of hard-shelled invertebrates) and as a result, represent modifications that separate

Kindleia from the more generalized predaceous line that gave rise to Amia.

Kindleia fragosa existed in the Late Cretaceous and Paleocene of North America in clear, slow-moving, fresh water streams and tributaries that bordered a retreating sea. The area was relatively low, containing both marshy areas and more elevated forested areas in a warm - temperate environment.

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APPENDIX

BONE	MEASUREMENTS (mm.)	UA 5398	UA 5401	UA 5402	UA 5404	UA 5416	UA 5417	UA 5421	UA 5423	UA 5426	UA 5429	UA 5435	UA 5439	UA 5449	UA 5450	UA 5453	UA 5456	UA 5457	UA 5460	UA 5476	UA 5480	UA 5481	UA 5482	UA 5483	UA 5486	UA 5487	UA 5492	UA 5493	UA 5494	UA 5499	UA 5501	UA 5503	UA 5504	UA 5505	UA 5506	UA 5507	Average for Kindlaia	Average for Amia from 7
EXTRASCAPULAR	length	9				8.5								6									8		8							7				8	10
	minimum length	3.5				3.5								2											3							2.5				3	4
	width	23				21								18									22		17							17				20	21
PTEROTIC	length	25				22		20		19					16		22		7								19									20	23
	width	10				10		10		8					6		7										6									8	9
	minimum width	2				3		3		2					2				2								2									2	3
PARIETAL	length	13				13		13		12					10		12																			12	18
	width	15				14		11		12					9		14																			12	13
FRONTAL	length	19						36							26		30																		29	30	35
	width							18		16					11		14																		12	15	18
	minimum width			9				9							6.5		8																		6	8	11
	depth of orbital excavation			3				3							3.5		2																		3	3	1
DERMOSPHENOTIC	length	12													10				10									10								10.5	14
	width	5													4				5									2.5								4	5
MAXILLA	length												32																				30			31	36
	width												6.5																				6			6	7
	# of teeth																																25			25	34
SUPRAMAXILLA	length								16				14																							5	19
	width								3.5				3																							3	4
LACRIMAL	length										12																									12	13
	width										8																									8	9
POSTERIOR SUBORBITAL	length								10																											10	8
	width								4																											4	4
	minimum width								2.5																											2.5	2
DORSAL POSTORBITAL	length	28																			20						18						23			22	30
	width																				9												7			8	14
	minimum width	7																			7						6	5				6			6.5	4.5
VENTRAL POSTORBITAL	length	29																			23									23			23			24.5	25
	width	20																			15									16			17			17	11
	minimum width	5																			4									6						5	6
PREOPERCULUM	length	9																			8															8.5	8
	width	42																			36															39	40
VOMER	length			15												10													12				12		17		13	21
	width			4	5											6													6				5		7		5.5	7
	approx. # of teeth			16+	18+																												25		25		25	18
ANTERIOR DERMOPALATINE	length				6													8				8							7				7	8	6	7	9
	width				5													6				5							5				6	6	5	5.5	5
	approx. # of teeth				20+													24															18+			5	24	20
POSTERIOR DERMOPALATINE	length				6																	6							6						6	6	12
	width				5																	3							5						5	4.5	4
	approx. # of teeth				25																															25	6
PARASPHENOID	length																																45		60	52.5	40
	width																																7		12	9.5	11
BASIOCCIPITAL	length																							13											14	13	18
	width																							9											11	10	13
	thickness																							4											5	4.5	5
OPISTHOTIC	length																																		15	15	12
	width																																		14	14	11
OPERCULUM	length	29				28															26												27		24	26.5	29
	width																				24												29			27	27
INTEROPERCULUM	length																									9										9	22
	width																									15										15	12
BRANCHIOSTEGAL RAYS	length of dorsal		16									16					23																	30			26.5	36
	width of dorsal		4									3					7																	8			7.5	10
	length of ventral											16																						16			16	18
	width of ventral											3																						3			3	6
GULAR	length																																	27	38		32.5	39
	width																																	12	22		17	19
DENTARY	length																				41												47	36	49	42	43	50
	width																				12												13	12	14	14	13	18
	approx. # of teeth																				16													14	15	15	15	15
ANGULAR	length																				18														17	18	18	22
	width																				13														13	12	13	15
SURANGULAR	length	6																																	7		3.5	6
	width	3																																	4		6.5	5
ANTERIOR CORONOID	length				7																10								8				11	10	12	10	9.5	7
	width				5																															5	5	4
	# of teeth																																			14	12	14
POSTERIOR CORONOID	length												6								8												7		10	6	7.5	6
	width																																			4	4	3
	# of teeth												8+																							10	10?	13
HYOMANDIBULAR	length at dorsal edge					12																															12	16
	width					22																															22	25
SUPRASCAPULAR	length	14				13																		11											15		13	14
	width	23				25																		19											22		22	25
SUPRACLEITHRUM	length	10				8	10																														10	10
	width	29				23	29																														29	29
METACLEITHRUM	length	7																		7										9							7.5	7
	width	17				14														14										15							15	14
CLEITHRUM	length																																		60	60	53
	width																																		36	36	26

TABLE 1. Table or measurements.

Fig. 1. UA 5398, dorsal and left sides of the posterior part of the skull (x 1).

Fig. 2. UA 5416, part of the dorsal and left sides of the posterior part of the skull (x 1.5).

Fig. 1. UA 5450, nearly complete dorsal roof of the skull (x 2).

Fig. 2. UA 5456, nearly complete dorsal roof of the skull (x 1.5).

Fig. 3. UA 5480, nearly complete right side of the skull (x 1).

Fig. 1. UA 5504, UA 5505, UA 5506, from left to right, respectively, ventral view of the skulls (x 1.25).

Fig. 2. UA 5506, nearly complete ventral side of the skull (x 1).

Fig. 1. UA 5402, right anterior part of the dorsal roof of the skull (x 3).

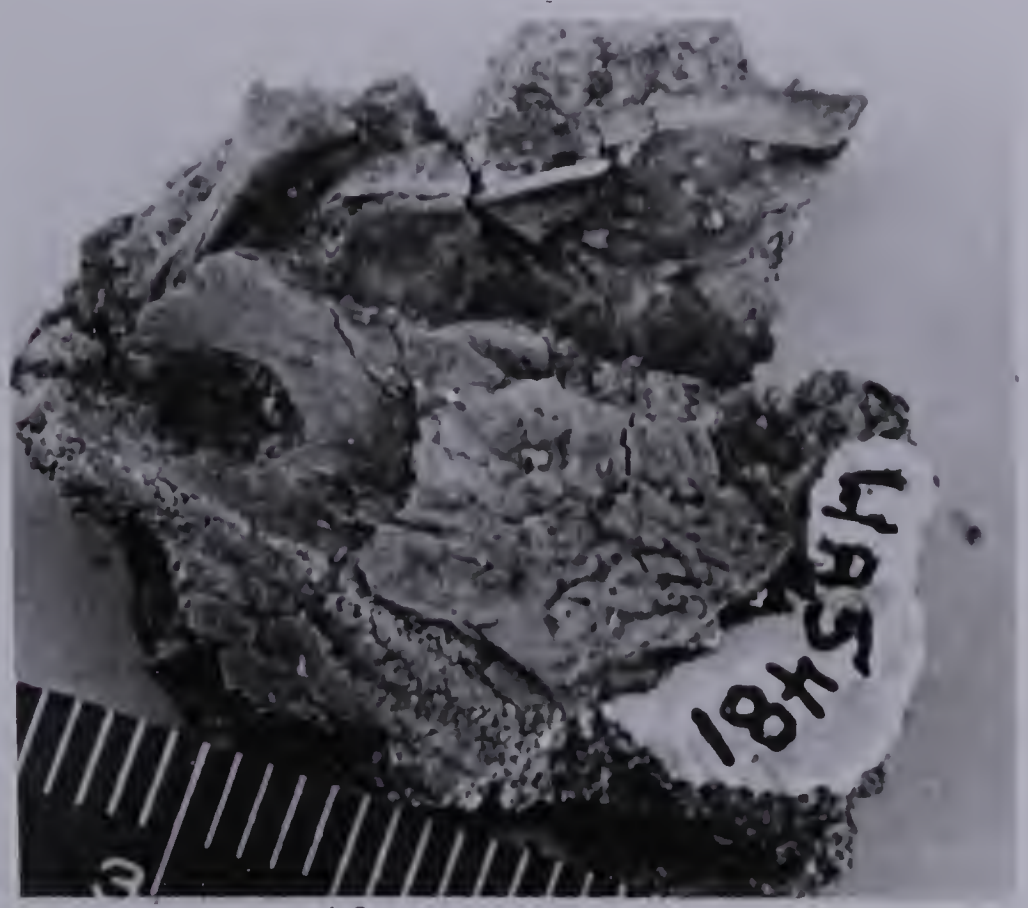

Fig. 2. UA 5481, dorsal view of a fragment of the anterior part of the skull, showing part of the skull roof and part of the palate (approx. x 3).

Fig. 1. UA 5406, ventral view of a fragment of the anterior part of the skull, with the gular missing (approx. x 3.5).

Fig. 2. UA 5439, internal view of part of the upper and lower jaws (x 2).

Fig. 3. UA 5402, palatal view of the vomers and the anterior part of the parasphenoid (x 3).

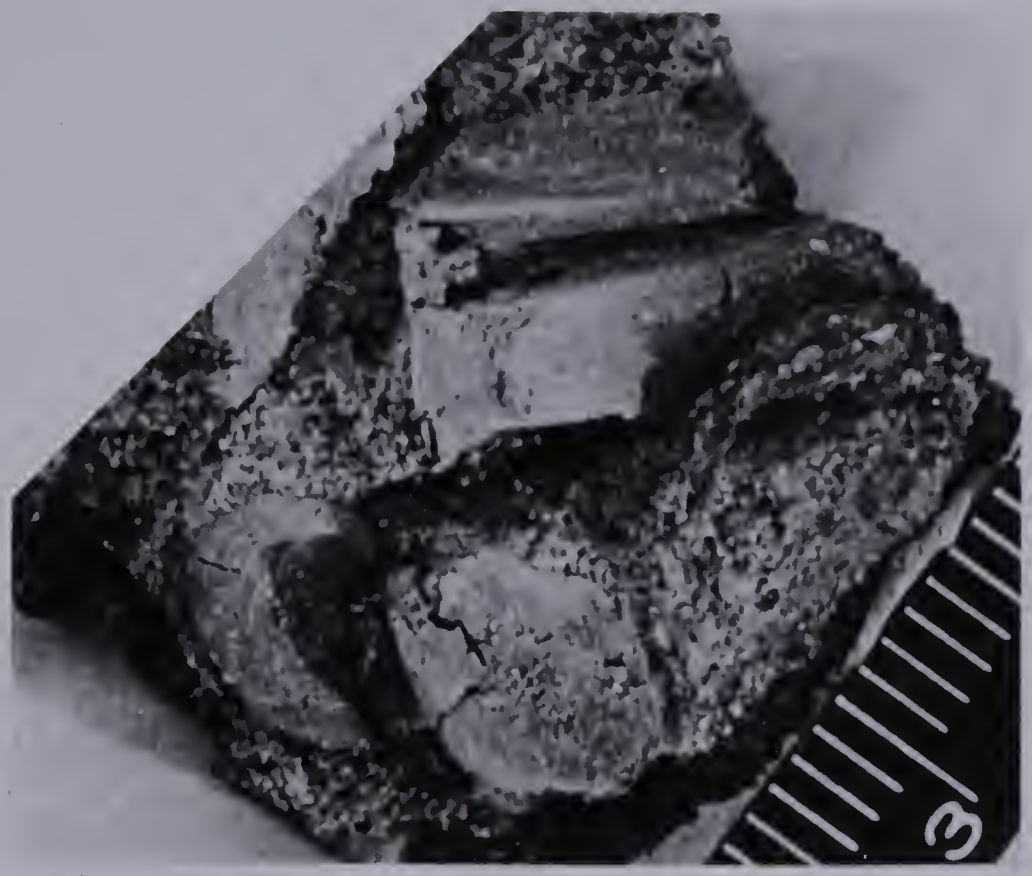

Fig. 1. UA 5483, ventral side of the basioccipital and the first two vertebrae (x 3).

Fig. 2. UA 5443, ventral view of the anterior trunk vertebrae (x 4).

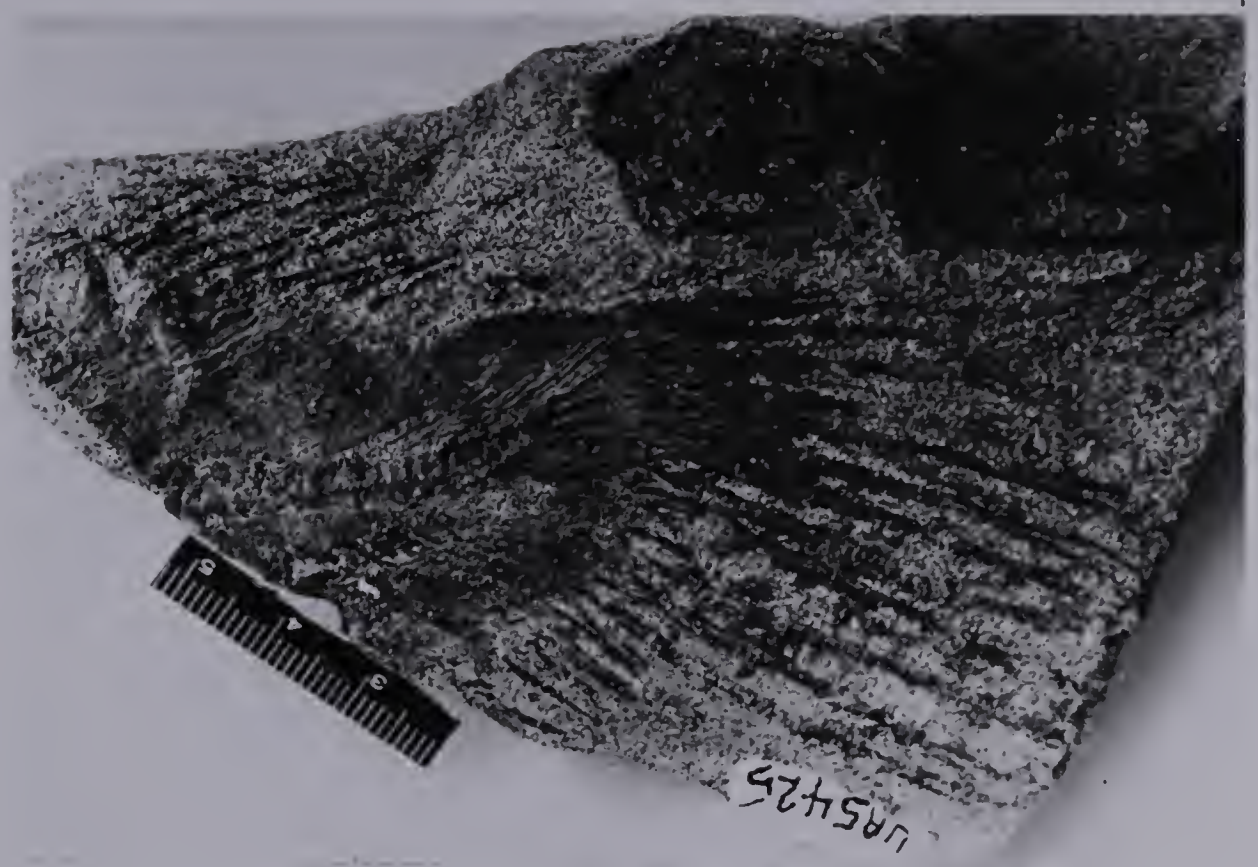

Fig. 1. UA 5425, tail and posterior part of the trunk (approx. x 1).

Fig. 2. UA 5475, fragment of the dermal covering of the trunk (x 1.5).